

PRELIMINARY PHYLOGENETIC STUDY OF BRADYBAENIDAE (GASTROPODA:
STYLOMMATOPHORA: HELICOIDEA)

Min Wu

Hebei University, Hezuolu 1, Baoding 071002, China;
minwu@mail.hbu.edu.cn

ABSTRACT

Morphological variation in the terminal genitalia of genera of Bradybaeninae is compared and discussed. This is the first attempt to study the anatomy of the endemic Chinese bradybaenids *Cathaica* (*Pliocathaica*), *Pseudiberus* (*Platypetasus*), and *Metodontia*. A preliminary phylogenetic analysis of bradybaenids was performed based on the character matrix from the present study. The focus was primarily on the terminal genitalia. *Helix* (Helicidae) and *Camaena* (Camaenidae) were used as outgroups. The results suggest that several previous taxonomic arrangements for the subdivision of this family, based on the analyses using shell features and/or superficial anatomy of genital system, are unsuitable. The cladistic analysis suggests that the use of the subfamily Helicostylinae, *sensu lato*, might not be suitable for use as the sister group of the known Bradybaeninae.

Two new endemic genera from western China are described based on the comparison of the terminal genitalia: *Aegistohadra* n. gen. and *Eueuhadra* n. gen. They are monophyletic and are readily distinguished from other bradybaenids by a synapomorphy, the presence of penial caecum. *Nanina delavayana* Heude, 1885, is designated as the type species of *Aegistohadra*. The type species of *Eueuhadra* is a new species, *E. gonggashanensis*.

Key words: Stylommatophora, Helicoidea, Bradybaenidae, China, terminal genitalia, phylogeny, phylogenetic analysis, new taxa.

INTRODUCTION

The Bradybaenidae (= Bradybaenidae + Helicostylidae, *sensu* Schileyko 1991) are a large group of terrestrial snails widely distributed in eastern Asia, with one species in Europe. Historically, more than 150 authors (Richardson, 1983; Wu, unpublished catalogue) have published on Chinese bradybaenids. However, most work on the classification of higher taxa of China was based on shell, not anatomical characters (Pilsbry, 1888–1894; Möllendorff, 1899; Dautzenberg, 1914–1915; Bavay & Dautzenberg, 1900, 1915; Blume, 1925; Ping & Yen, 1932; Yen, 1939; Zilch, 1940; almost all previous work). Therefore, knowledge on the bradybaenid systematics has remained unsatisfactory.

The monograph by Wiegmann (1900), in which species from 12 genera and subgenera are described, was the first study dealing specifically with the anatomy of bradybaenid genitalia. More recently, some malacologists have made comparative studies of the genital mor-

phology, mainly based on their native bradybaenid taxa (Schileyko, 1978; Azuma, 1982; literature of Japanese workers, cited by Nordsieck, 2002; Lee & Kwon, 1993, 1994; Wu, 2001; Wu & Guo, 2003). Many authors have focused on the general structures, such as the size of dart sac, the presence/absence of a flagellum, and the number of mucous glands. Schileyko (1978) gave a much more precise, detailed description of the terminal genitalia of Russian bradybaenids that includes the above traditionally described character and internal dissections of the penis and dart apparatus. More recently, Nordsieck (1987) stated that the bradybaenid groups are characterized by apomorphies of the genital organs.

However, similar work covering most endemic Chinese bradybaenid taxa, which is essential for understanding the general anatomy of bradybaenids and construction of a sound taxonomic framework, has been lacking.

The present work compares the structure of the terminal genitalia of some genera of the

Bradybaenidae based on dissection of their type species or non-type congeners. Two new bradybaenid genera are proposed based on anatomical and shell characters. A preliminary phylogenetic analysis is performed based on the data obtained from these dissection results. This phylogeny is compared to the three bradybaenid subdivision plans comprehensively reviewed recently by Nordsieck (2002), widely used thus far in China (e.g., Yen, 1939; Zilch, 1960), Russia (e.g., Schileyko, 1978), and Japan (e.g., Kuroda & Habe, 1949; Minato, 1988).

MATERIALS AND METHODS

This study is based on specimens from the collections of the Zoological Museum, Institute of Zoology, Chinese Academy of Sciences (IZCAS), and from those belonging to Forschungsinstitut und Naturmuseum Senckenberg (SMF). Many genera are represented by the non-type congeners rather than by the type species, because of the paucity of alcohol-preserved specimens in museums and the absence of specimens from type localities.

All examined specimens (except specimens of IZCAS00067, which were first fixed in formalin before being placed in 70% ethanol) are preserved in 70% ethanol. For preparing the dissections, a tiny hole was carefully drilled into the shell apex to assist removal of the soft parts of the snail using water pressure. All the illustrations were drawn using a stereo microscope and camera lucida. Shell and genital measurements were taken with 0.01 mm and 0.1 mm accuracy respectively for the new taxa described. Whorl number was counted as described by Kerney & Cameron (1979) and was taken with 1/8 whorl accuracy. Both color and length of soft parts in the descriptions refer to those observed and measured after alcohol preservation. Type specimens of the new species are deposited in IZCAS, Beijing.

Taxa studied are listed in Appendix I along with locality data and museum accession numbers. Descriptions of new taxa are given in Appendix II.

Abbreviations

The abbreviations used in the text and in the illustrations are explained as: ADC – channel connecting accessory sac and dart sac; AG – albumen gland; App – vaginal empty appen-

dicula; AS – accessory sac (= inner stylophore in Giusti et al., 1992); ASC – accessory sac chamber; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; C23 – chamber produced by V2 and V3 in dart sac; DS – dart sac (= outer stylophore in Giusti et al., 1992); Dt – love dart; DtC – chamber containing the dart = dart sac chamber; DVM – membranous sac surrounding dart sac and/or distal region of vagina near atrium (= basal genital sheath in Cuezco, 1998). When preparing the genitalia for observation, the structures were carefully preserved for future examination.

Ep – epiphallus, the region between the penis and the insertion of the vas deferens. The delimitation is easily recognized when the epiphallallic papilla (= verge in Cuezco, 1998: 102) is present. When the epiphallallic papilla is lacking, the continuous ridge structure can help to distinguish the epiphallallic region from that of penis (Cuezco, 1998). It is notable that the concept used by Cuezco (1998) differs from that used by Giusti et al. (1992), who defined the epiphallus as “from end of vas deferens to point of attachment of penial retractor”. The term epiphallus of Cuezco (1998) is used here, because the point of attachment of penial retractor varies among different bradybaenid groups, and in most cases it is not level with the epiphallallic papilla.

EpP – epiphallallic papilla (= “penial” verge in Schileyko, 1991); MAC – mucous gland-accessory sac channel; MG – mucous gland (= dart gland in Nordsieck, 2002); OD – oviduct; Ov – ovotestis; P – penis; according to the epiphallus concept used by Cuezco (1998), the term penis used in this study refers to the region between the epiphallallic papilla and the atrium, or when the epiphallallic papilla is absent, it refers to the region close to the atrium and internally possesses the similar and continuous pilaster/ridge structure.

PLs – polylayered structure in dart sac and/or accessory sac, produced by wavy and spongy connective tissue. PLs is not separate, but connected tightly with neighboring tissue, and if present, is visible when the dart apparatus is dissected sagittally. This structure occurs as occupying most part of dart sac (e.g., in Fig. 14C) or a small and limited region (e.g., in Fig. 11B) in the dart apparatus; PR – penial retractor muscle; PS – penial sheath; PP – penial pilaster(s)/ridge(s); SPC – simple penial caecum; T – talon; UV – free oviduct; Va – vagina; VD – vas deferens; V1 – a valvule opposite the opening of mucous glands, in sag-

ittal plane of dart sac (as in Fig. 6D); V2 – a valvule opposite V1 and closest to atrium, together with V1 forming a muscular tube containing dart(s) (as in Fig. 6D); V3 – a valvule between V2 and V4, in sagittal plane of dart

sac (as in Fig. 6D); V4 – most inner/proximal valvule in DC, together with V1 forming a chamber containing love dart(s) (as in Fig. 6D). Terms V1–V4 are employed, for convenience only, to show the sagittal plane of dart sac.

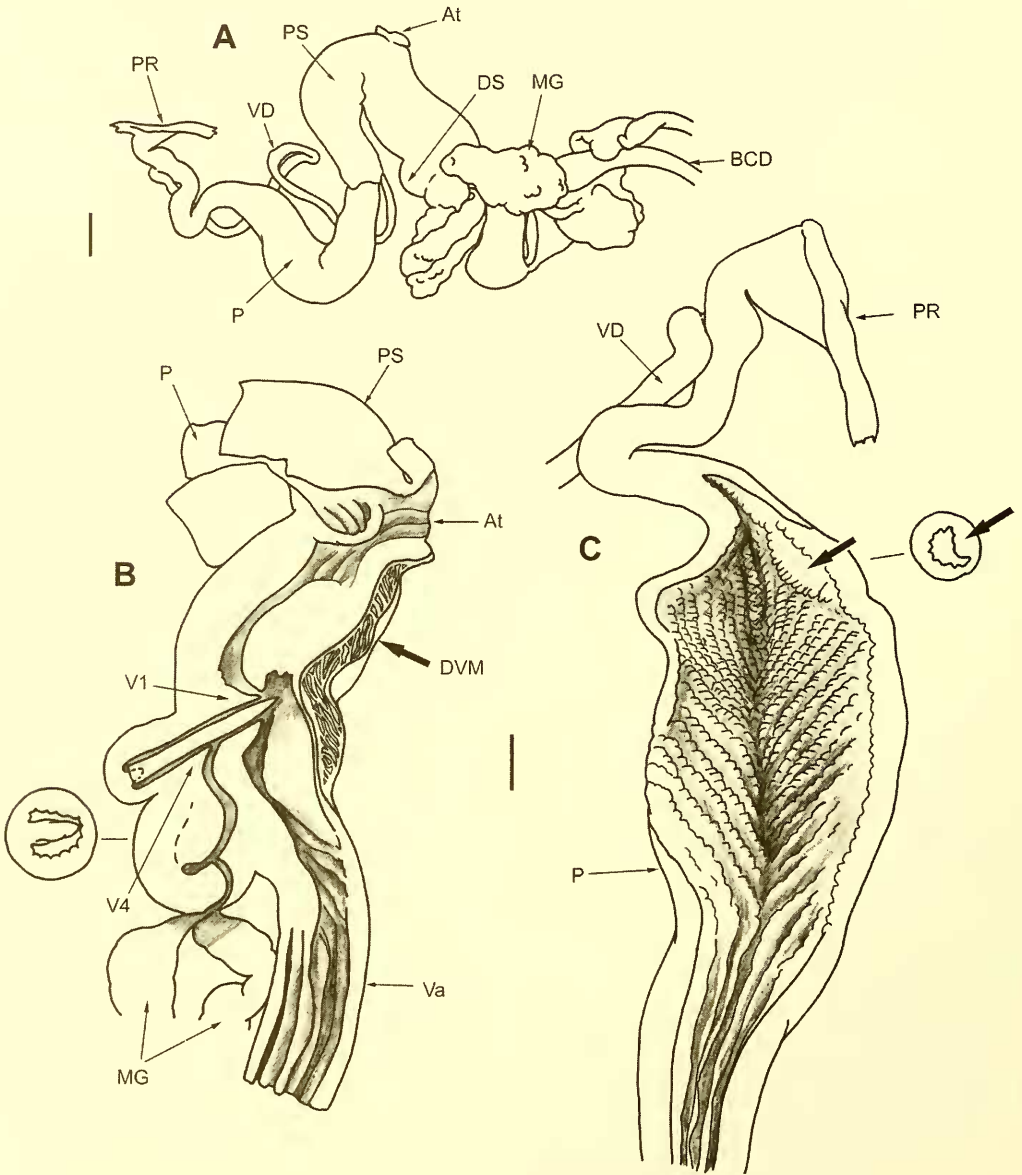


FIG. 1. *Fruticicola fruticum* (O. F. Müller, 1774), IZCAS01009-2. A, general view of genitalia; B, dart sac and part of vagina, sagittal section, with cross-section of accessory sac. Structured DVM indicated by a thick solid arrow; C, penis, opened, with cross-section, showing a fold formed by the penial pilasters. A & B showing the elongated vagina section between dart sac and atrium. Bars equal 1 mm.

Each view of the three dimensional portrayal represents only one part of the boundary of the chamber near it.

Cladistic Analysis

Cladistic analyses were performed using the computer program Hennig86 Version 1.5 (Farris, 1988) and program Winclada Version 1.00.08 (Nixon, 2002). The analysis of the character distribution on the cladograms was carried out using the program Winclada.

All the 28 characters used, observed from terminal genitalia except Character 27 from mantle, are based on a selection made after my study of the representatives for terminal groups. Of the characters (0–27), seven binary characters and the remaining multistate characters were coded as non-additive. To avoid artificial judgement, character polarity is obtained as one of the results of the analysis rather than as an apriori assumption (Nixon &

Carpenter, 1993). Therefore, all characters involved are treated as undirected and unordered. No missing character state occurred in the examined terminals (Table 1). Considering that fused coding involves a loss of phylogenetic information (Lee & Bryant, 1999), the inapplicable characters (e.g., coding of character 1 was separated from that fused with character 0) were separately coded when the character-variable is inapplicable in some taxa.

Selection of the Ingroup and Outgroup Taxa

Besides including two newly proposed genera, the ingroup bradybaenid taxa considered were those included in the subfamily Bradybaeninae by Richardson (1983), except *Armandiella* Ancey, *Tricheulota* Pilsbry, *Plecteulota* Möllendorff, *Neseulota* Ehrmann, *Archaeoxesta* Kobelt, *Cocoglypta* Pilsbry, *Coneulota* Pfeffer, *Dolicheulota* Pilsbry, and *Ponsadenia* Schileyko, because alcohol-pre-

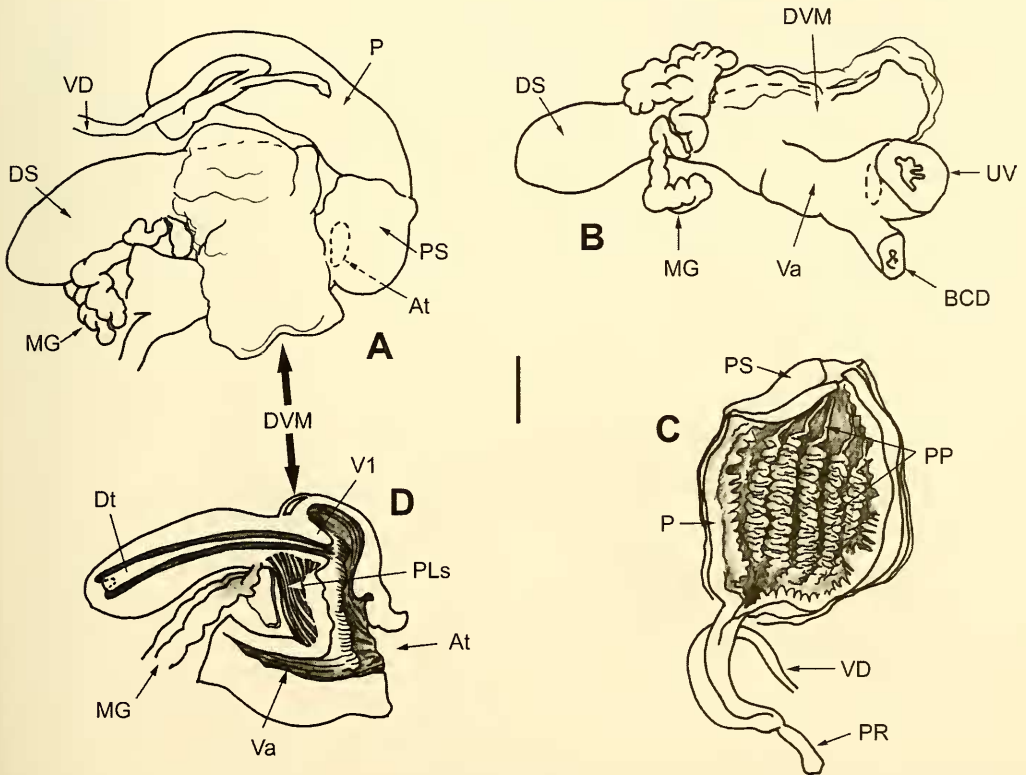


FIG. 2. *Bradybaena similaris* (Rang, 1831), IZCAS01072-1. A, lateral view of dart apparatus and penial complex; B, basal view of dart apparatus; C, penis, opened; D, dart sac, sagittal section. DVM indicated by thick solid arrows in A & D. Bar equals 1 mm.

served material was unavailable. *Semi-buliminus* Möllendorff was excluded because it was recently grouped into *Metodontia* (Wu, in review). *Halolimnohelix* Germain, *Haplohelix* Pilsbry, *Urguessella* Preston, and *Vicarihelix* Pilsbry listed in Richardson's bradybaenid catalog (1983; also in Thiele, 1931) were excluded because they are, on the basis of anatomy, non-bradybaenid helicoids (Nordsieck, 1986, 1987; Schileyko, 1991).

Results of previous cladistic analyses for Helicoidea were used as the departure point for outgroup selection. According to the cladogram based on a molecular database

(Wade et al., 2001: fig. 3c), the Camaenidae–Helicidae–Polygridae group forms the sister group of Bradybaenidae. In another anatomy-based cladistic analysis of Xanthonychidae (= Helminthoglypidae; Cuezco, 1998), the sister relationship of the Bradybaenidae and Xanthonychidae–Helicidae groups are supported by four synapomorphies. Therefore, in this study, the Helicidae and Camaenidae were chosen as outgroups.

All the 23 genera and subgenera were treated as separated terminal taxa. The type species was available for only 11 ingroup and one outgroup genera. These are: *Acusta*,

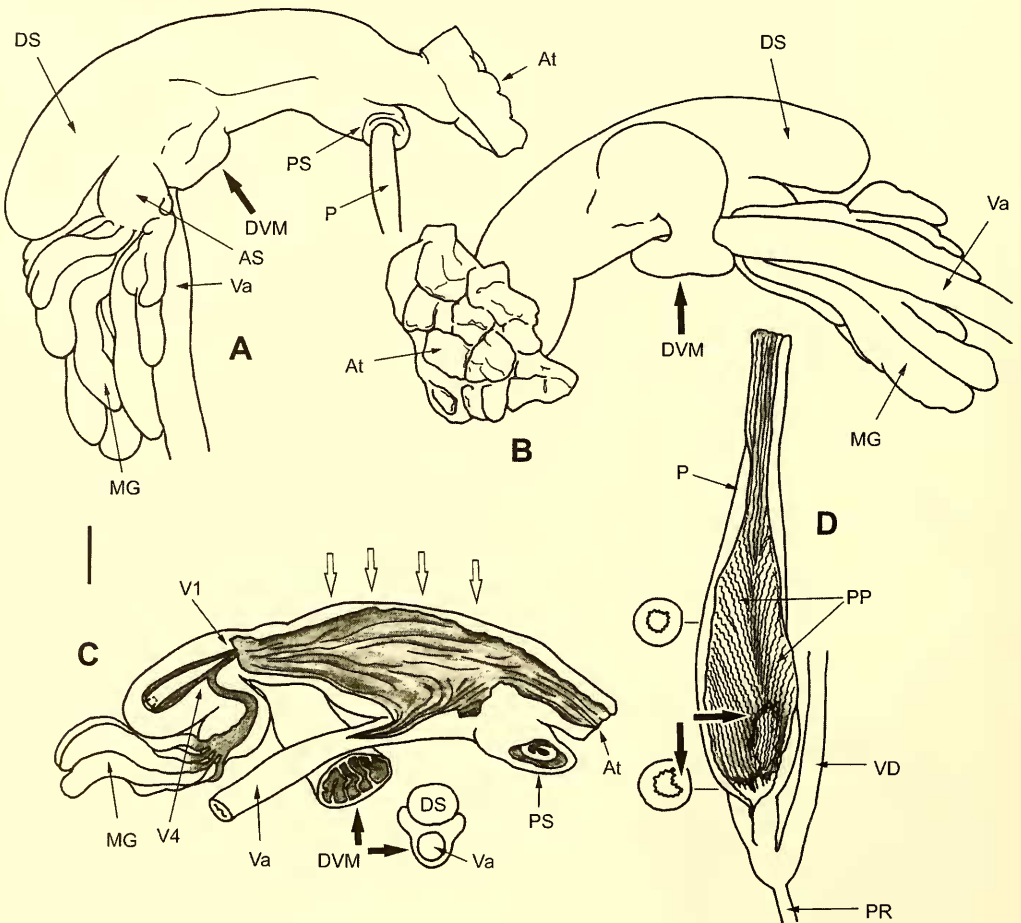


FIG. 3. *Karafothelix weyrichii* (Schrenck, 1867), IZCAS01080-2. A, B, lateral views of dart sac, DVM indicated by thick solid arrows; C, dart sac, sagittal section, with cross-section showing DVM, DVM indicated by thick solid arrows, neck-structure indicated by thick hollow arrows; D, penis, opened, with cross-sections, fold formed by the penial pilasters indicated by thick solid arrows. Bar equals 1 mm.

Bradybaena, *Cathaica*, *Fruticicola*, *Mastigeulota*, *Pseudaspasita*, *Nesiohelix*, *Aegistohadra* n. gen., *Eueuhadra* n. gen., *Trichobradyla*, *Pfeifferia*, and *Helix*. Otherwise, only those species commonly accepted in a group were used as the representatives for their generic group.

RESULTS

Character Descriptions

Character 0: Presence of the membranate sac surrounding the dart sac and/or the distal region of the vagina near to the atrium (DVM).

(0) absent; (1) present (Figs. 1B, 2A, 2D, 9A, indicated by thick solid arrows).

Remarks: The dart sac is inserted on the vagina. In very few cases, the dart sac is basally wrapped by a layer of membrane, which sometimes appears to be sac-like (Fig. 3A–C, indicated by thick solid arrows) near the atrium, completely or partially.

Character 1: The DVM internally simple or structured:

(0) not applicable because DVM absent; (1) DVM present, internally simple (Figs. 2A, 2D, 9A, indicated by thick solid arrows); (2) DVM present, internally structured, with numerous cells (Figs. 1B, 3C, indicated by thick solid arrows).

Character 2: The proximal dart sac and/or the distal region of the vagina are/is wholly encircled by the DVM or not:

(0) not applicable because DVM absent; (1) DVM present, proximal dart sac partially encircled by DVM (Figs. 1B, 3B, C, indicated by thick solid arrows); (2) DVM present, proximal dart sac wholly wrapped by DVM (Fig. 2A, indicated by thick solid arrows).

Character 3: Presence of the penial sheath:

(0) absent; (1) present.

Remarks: In *Nesiohelix swinhoei*, *Aegistohadra* n. gen., *Eueuhadra* n. gen., *Pfeifferia micans*, and *Calocochlea coccomelos*, the penial sheath is lacking (Figs. 5D, 6A, C, 7A, B, 8A, B, 9A, D). In the other genera, the penial sheath is always present (e.g., Azuma, 1982). In the outgroup *Helix pomatia*, the penial sheath is present and developed, wrapping the whole penis and the basal part of penial retractor (Fig. 10D, E, indicated by thick solid arrows). In bradybaenid genera, the penial sheath, if present, cannot be morphologically distinguished from that of *Helix*.

Character 4: Differentiation status of the penial pilasters:

(0) penial pilasters not differentiated; (1) penial pilasters differentiated near epiphallus;

(2) penial pilasters differentiated near atrium.

Remarks: Differentiated penial pilasters are those thickened, deep, and/or morphologically distinguishable from the neighboring zig-zag ones of moderate thickness. In most species examined, the penial pilasters are somewhat thickened near the epiphallus, becoming thinner near the atrium (e.g., Figs. 2C, 11C, 12C, 13C, 14E, 15D). It is characteristic that the pilasters on the penial inner wall differentiate towards the atrium or to-

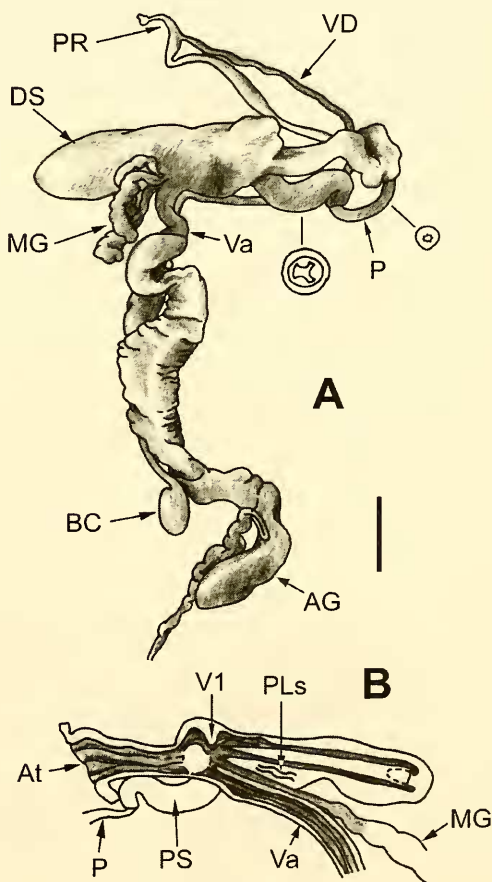


FIG. 4. *Metodontia yantaiensis* (Crosse & Debeaux, 1863), IZCAS00131-1. A, general view of genitalia, with cross-sections of penial sheath and penis; B, dart sac, sagittal section. Bar equals 1 mm.

wards the epiphallus. In *Fruticicola fruticum* and *Karaffohelix weyrichii*, the penial pilasters differentiate near the epiphallus and form an asymmetrically projecting fold (Figs. 1C, 3D), which is similar to the asymmetrical epiphallic papilla of *Nesiohelix swinhoei*

(Fig. 5E), and assumed to serve as the epiphallic papilla. In *Stilpnodiscus moellendorffi* (Fig. 16B), *S. yeni*, *S. entochilus*, and *Laeocathaica (Laeocathaica) subsimilis* (Fig. 17B), the penial pilasters become thickened and differentiated near the atrium. Especially

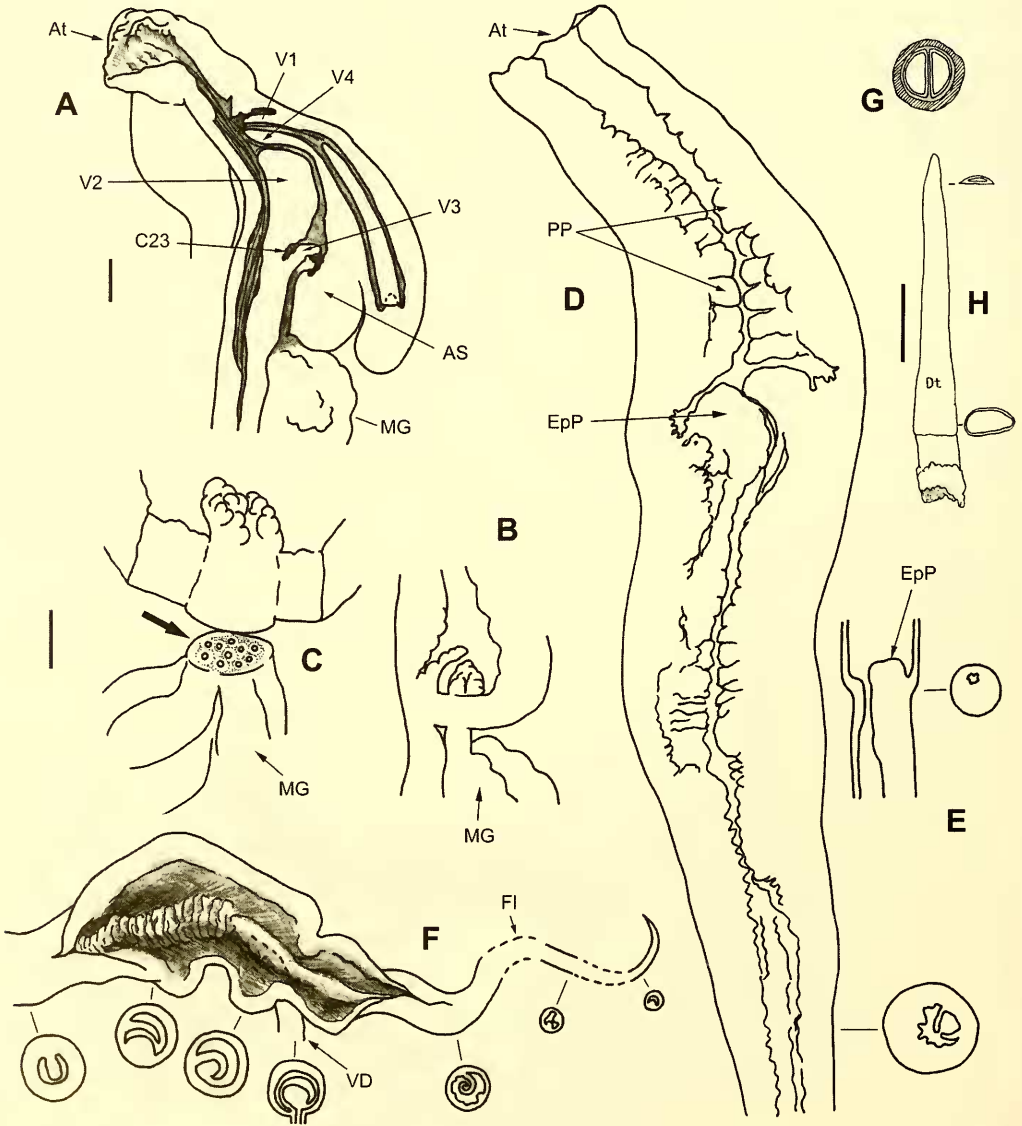


FIG. 5. *Nesiohelix swinhoei* (L. Pfeiffer, 1865), IZCAS00055-2. A, dart sac, sagittal section; B, sagittal section of accessory sac; C, cross section of mucous glands insertion on accessory sac, mucous tube entrance indicated by a thick solid arrow; D, penis and epiphallus, sagittal section, with cross-section of epiphallus; E, sagittal section of penis-epiphallus region, diagrammatic, with cross-section; F, epiphallus and flagellum, opened, with cross-sections; G, cross-section of dart sac, showing two pieces of dart; H, a piece of dart, with cross-sections. Bars equal 1 mm.

in *Stilpnodiscus*, such differentiated pilasters are high and valvule-shaped.

Character 5: Presence of the epiphallic papilla:
 (0) epiphallic papilla absent (e.g., Fig. 11C);
 (1) present (e.g., Fig. 12C).

Character 6: Symmetry of the epiphallic papilla (EpP):

(0) not applicable because epiphallic papilla absent;
 (1) epiphallic papilla present and symmetric (e.g., Figs. 12C, 13F); (2)

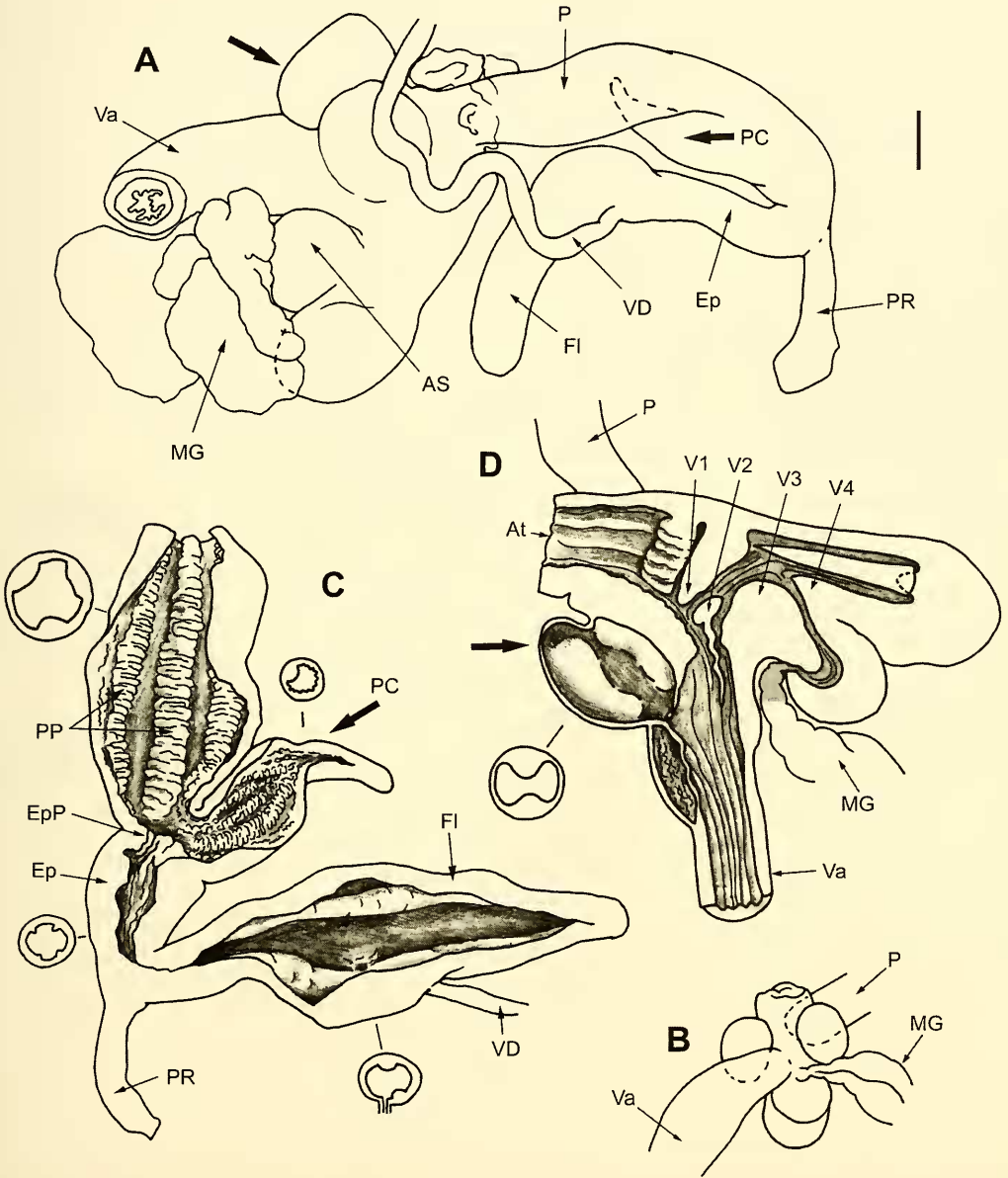


FIG. 6. *Aegistohadra delavayana* n. gen. & comb., IZCAS00132-3. A, general view of terminal genitalia, the sac of vagina opposite to dart sac indicated by a thick solid arrow (left), penial caecum indicated by a thick solid arrow (right); B, basal view of dart sac, diagrammatic; C, penial complex, opened, with cross-sections, penial caecum indicated by a thick solid arrow; D, dart sac, sagittal section, the sac of vagina opposite to dart sac indicated by a thick solid arrow. Bar equals 1 mm.

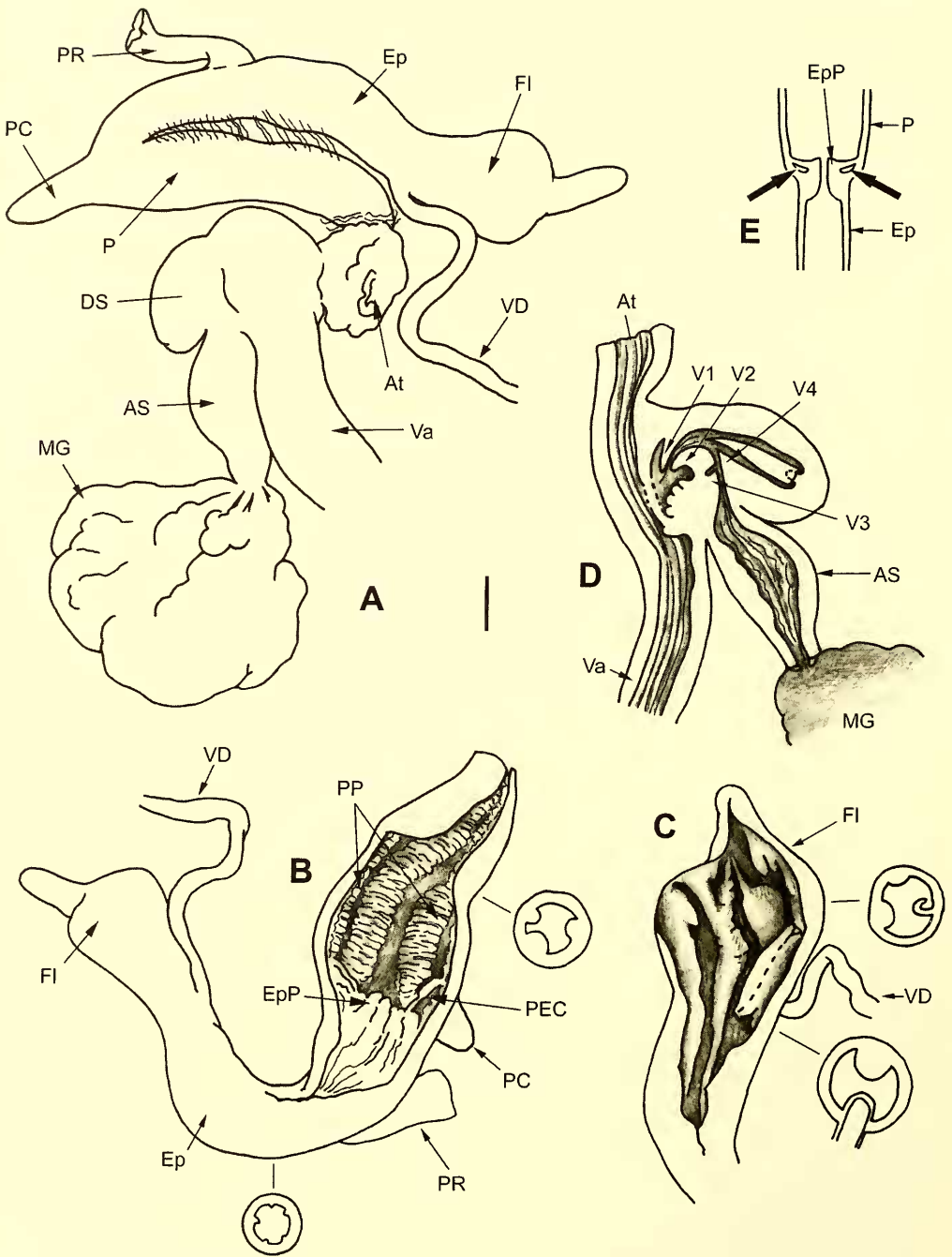


FIG. 7. *Eueuhadra gonggashanensis*, n. gen. & sp., IZCAS00067-13, Paratype. A, general view of terminal genitalia; B, penial complex, penis and partially epiphallus opened, with cross-sections; C, epiphallus and flagellum, opened, with cross-sections; D, dart sac, sagittal section; E, section of penis-epiphallus region, diagrammatic. Bar equals 1 mm.

epiphallic papilla present and asymmetric (Figs. 5E, 8D, 9D).

Remarks: In *Nesiohelix swinhoei*, *Aegistohadra* n. gen., *Eueuhadra* n. gen., *Pfeifferia micans*, *Calocochlea coccomelos*, *Cathaica (Pliocathaica) gansuica*, *Aegista (Aegista) accrescens*, *Aegista (Plectotropis) gerlachi*,

Laecathaica (Laecathaica) subsimilis, *Acusta ravidata*, *Trishoplita dacostae*, and *Euhadra herklotsi* (Figs. 5D, 6C, 7B, 8D, 9D, 12C, 13F, 14E, 17B, 18D, 19D, 20C), a more or less protruding epiphallic papilla is present. In the remaining bradybaenid genera the epiphallic papilla is depressed or missing.

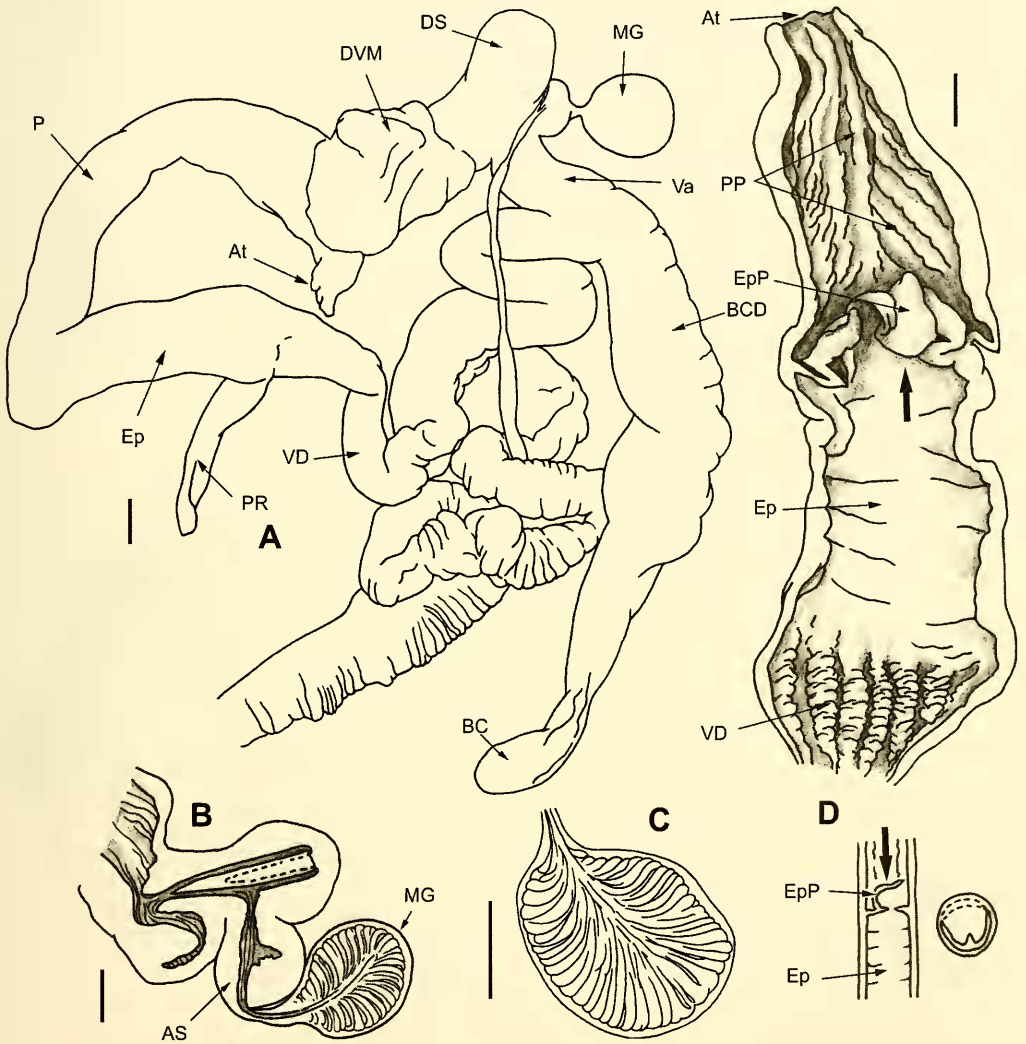


FIG. 8. *Calocochlea coccomelos* (Sowerby, 1840), SMF 323619. A, general view of genitalia; B, dart sac, sagittal section; C, mucous glands, sagittal section; D, above: Penis-epiphallus region, opened; below: cross-section of penis-epiphallus transition, diagrammatic; valve-shaped epiphallic papilla indicated by thick solid arrows. Bars equal 1 mm.

Character 7: The epiphallic papilla valve-shaped or papilla-shaped:

(0) not applicable because epiphallic papilla absent; (1) epiphallic papilla present, valve-shaped (Figs. 8D & 9D, indicated by thick solid arrows); (2) epiphallic papilla present, papilla-shaped (e.g., Figs. 5D, 10D).

Character 8: Presence of the penial caecum: (0) absent; (1) present (e.g., Figs. 6A, 6C, indicated by thick solid arrows).

Remarks: This structure can be easily distinguished from the following simple penial

caecum (SPC) by the PC pilasters, which are differentiated from those of the caecum. In the simple penial caecum (SPC), which characterizes the genera *Trichobrydaena* and *Mastigeulota*, the penial pilasters forming the inner wall of caecum are just the extended parts from its outer/entering pilasters.

Character 9: The simple penial caecum: (0) absent; (1) present (Figs. 11B, 23A, indicated by thick solid arrows).

Character 10: Presence of the flagellum: (0) absent; (1) present.

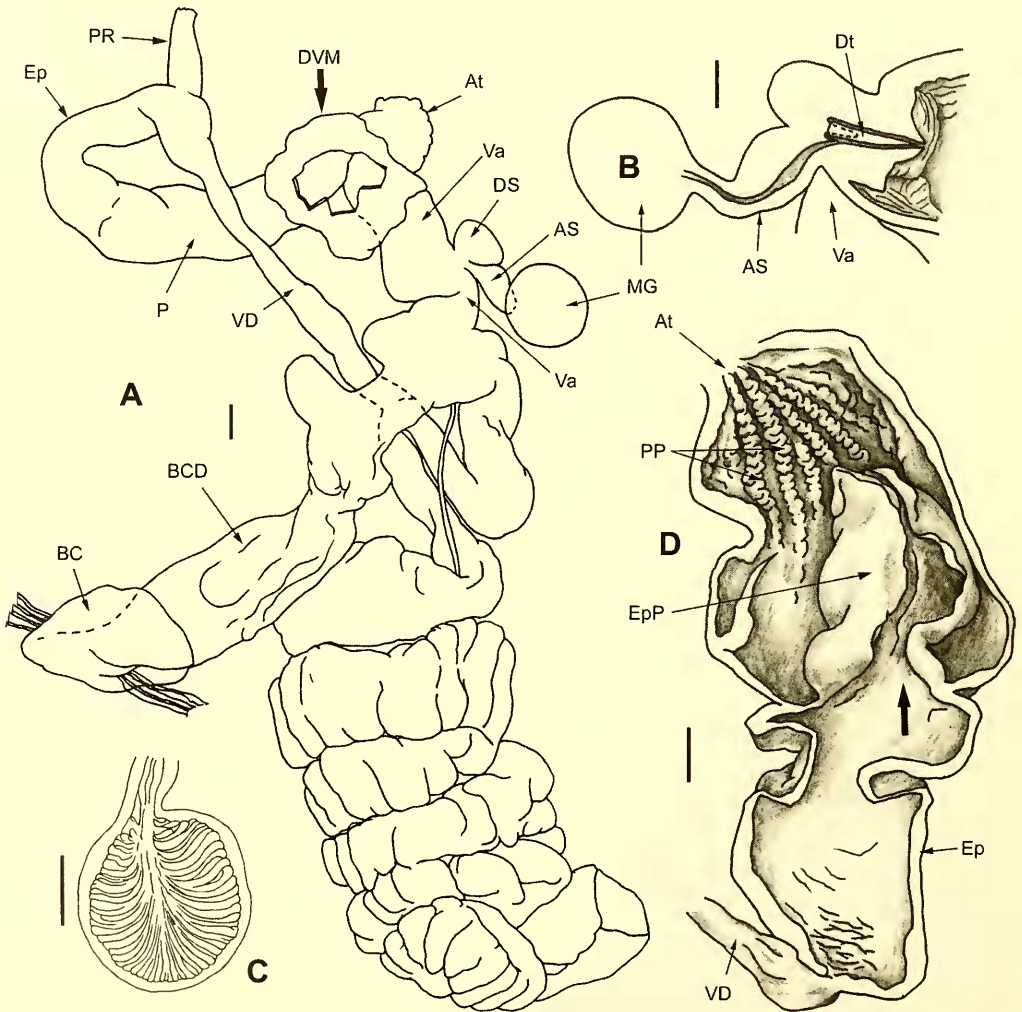


FIG. 9. *Pfeifferia micans* Pfeiffer, 1845, SMF 323620. A, general view of genitalia; B, dart sac, sagittal section except mucous glands; C, mucous glands, sagittal section; D, penis-epiphallus region, opened, valve-shaped epiphallic papilla indicated by a thick solid arrow. Bars equal 1 mm.

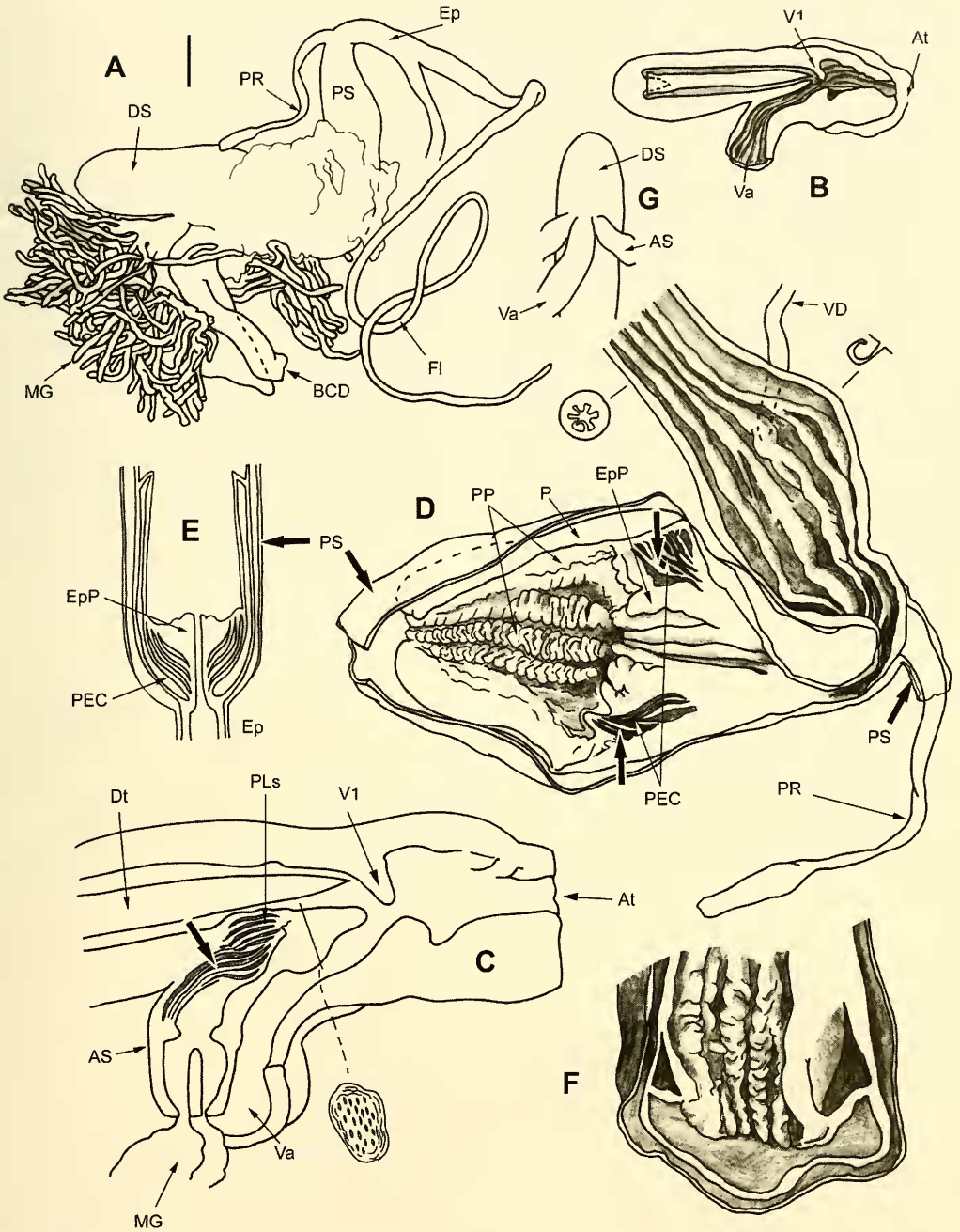


FIG. 10. *Helix pomatia* (Linné, 1758), IZCAS00188-1. A, general view of terminal genitalia, bar equals 2 mm; B, dart sac, sagittal section with mucous glands removed; C, section of partial dart sac, with cross-section; D, penial complex, opened, with cross-sections, middle two thick solid arrows indicating penis-epiphallus chambers; E, section of penis-epiphallus region, diagrammatic, penial sheath indicated by a thick solid arrow; F, distal penis near atrium opening, opened; G, basal view of dart sac, diagrammatic.

Remarks: The flagellum and the vas deferens insertion structure are almost the same in the species examined. Flagellum, if present, with inner ridges simple or somewhat complexly arranged. Insertion of vas deferens on flagellum inwardly forms a more or less distinct C-shaped (in cross-section) fold towards the tip of flagellum (Figs. 5F, 7C, 10D, 13D, 14F, 19E, 20A). The only exception is *Aegistohadra delavayana*, n. comb., in which a depressed pilaster instead of the distinct C-shaped fold is present (Fig. 6C). These structures are the same in bradybaenid genera and in *Helix pomatia*. Therefore, if present, the flagellum of the various groups examined might be considered homologous.

Character 11: Presence of the polylayered structure (PLs) in accessory sac:

(0) PLs absent (e.g., Figs. 1B, 5A, 8B); (1) PLs present (e.g., Figs. 2D, 10C, 11B, 13C, 14C, 22D); (2) not applicable because dart sac absent.

Remarks: In *Metodontia yantaiensis*, the accessory sac has some wavy and spongy

connective tissue (polylayered structure, PLs) (Fig. 4B). In *Pseudaspasita binodata*, such structure seems to be weakly developed (Fig. 21C). This kind of structure can be easily distinguished from the folds/pilasters on the inner wall of the accessory sac (Fig. 16E) by the compactness and parallelism in the arrangement of its filaments/layers. In *Bradybaena similis* and *Cathaica (Cathaica) fasciola*, the structure is much developed and situated between insertion of mucous glands and vagina (Figs. 2D, 22D). In *Aegista (Aegista)* it is highly developed and uppermost, and it wraps the dart chamber (DtC) (Figs. 13C, 14C). In *Aegista (Plectotropis)*, PLs occupies the whole accessory sac that is externally visible and the region between dart sac and the vagina. Interestingly, in *Helix pomatia*, the polylayered structure is also present, at the pit formed by both dart the sac and each of the accessory sacs/trunk of basal mucous stalks (Fig. 10C). The observed PLs of the taxa studied are provisionally assumed to

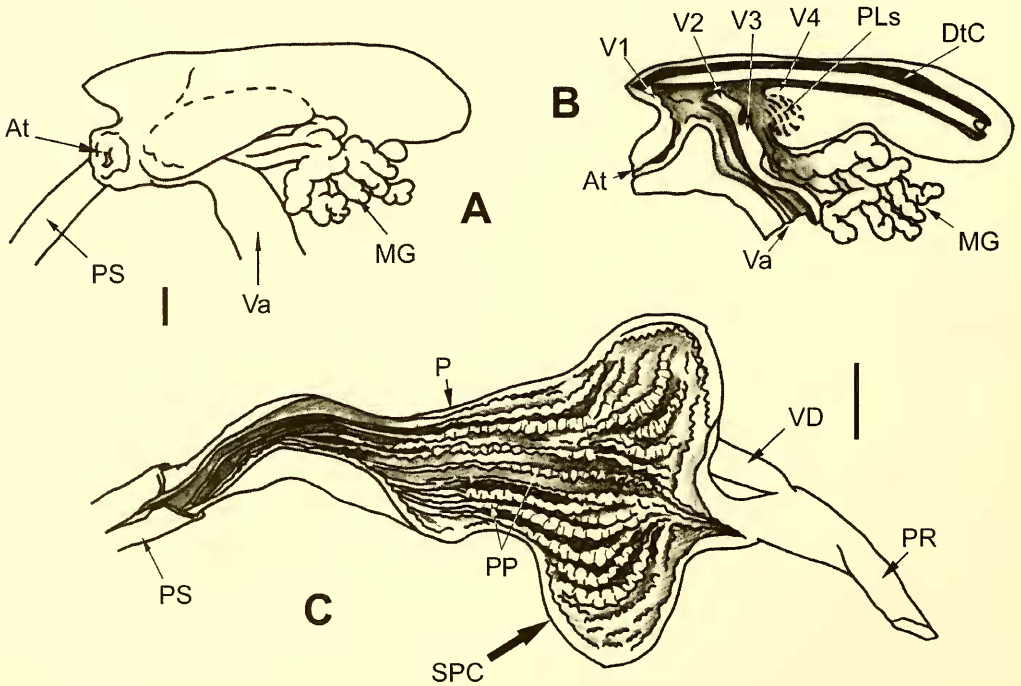


FIG. 11. *Mastigeulota kiangsinsensis* (E. Martens, 1875), IZCAS00003-1. A, lateral view of dart apparatus; B, dart sac, sagittal section; C, penis, opened, simple penial caecum (SPC) indicated by a thick solid arrow. Bars equal 1 mm.

be homologous in origin, because they occur only in the specific region in dart apparatus, and assumed to be related to dart shooting or pumping the mucus out during copulation.

Character 12: Distribution of polylayered structure (PLs) in accessory sac:

(0) not applicable because PLs absent; (1) distributed between mucous glands insertion

and vagina (region I) (e.g., Fig. 22D); (2) PLs present, distributed between mucous glands insertion and dart caecum (DtC; region II) (e.g., Figs. 4B, 10C, 11B); (3) PLs present at region I & II (e.g., Fig. 14C).

Character 13: The common entrance of mucous glands:

(0) mucous glands without common entrance (e.g., Figs. 19B, 20D); (1) with common en-

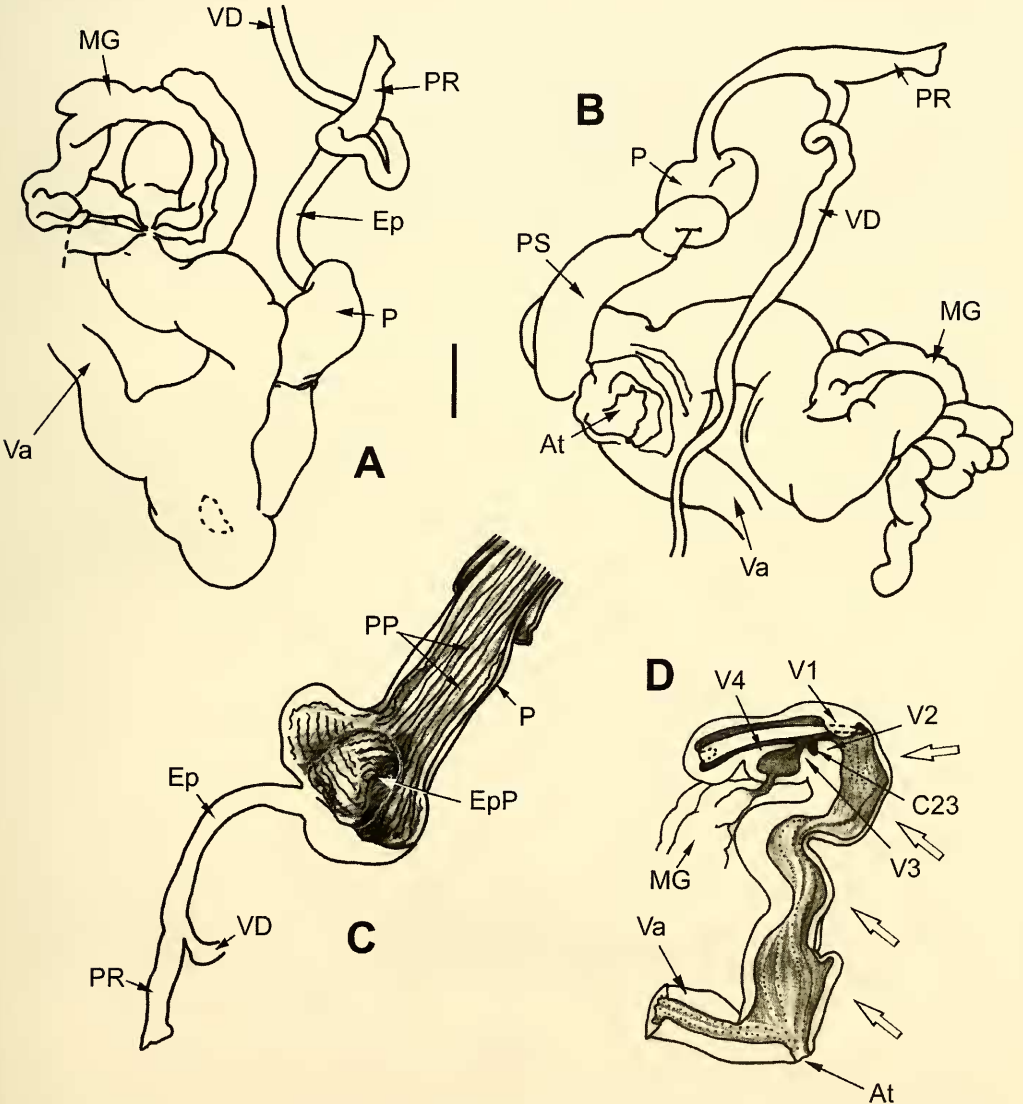


FIG. 12. *Cathaica (Pliocathaica) gansuica* (Möllendorff, 1899), IZCAS00210-1. A, basal view of dart sac and penial complex; B, lateral view of dart sac and penial complex; C, penis, opened; D, dart sac, sagittal section, neck-structure region of dart sac indicated by four thick hollow arrows. Bar equals 1 mm.

trance; (2) not applicable because dart sac absent.

Remarks: There are two ways by which the mucous glands are inserted on the accessory sac, which can only be observed when the accessory sac is cut open sagittally. Usually, the mucous glands open into the accessory sac through a common duct (Figs. 1B, 2D, 4B, 6D, 7D, 11B, 12D, 13C, 14C, 15C, 16C, 17C, 18B, 21C, 22D, 23E, 24B). Another situation was found in *Karaftohelix weyrichii*, *Trishoplita dacostae*, *Euhadra*

herklotsi, and *Nesiohelix swinhoei* (Figs. 3C, 5C, 19B, 20D), with two to numerous separate tubes rather than a common tube opening into the accessory sac.

Character 14: The distinguishability of the accessory sac from outside of the dart sac:

(0) indistinct from outside of the dart sac; (1) distinct from outside of the dart sac; (2) not applicable because dart sac absent.

Remarks: The accessory sac cannot always be distinguished externally by an apparent external boundary from the dart sac (e.g., Fig.

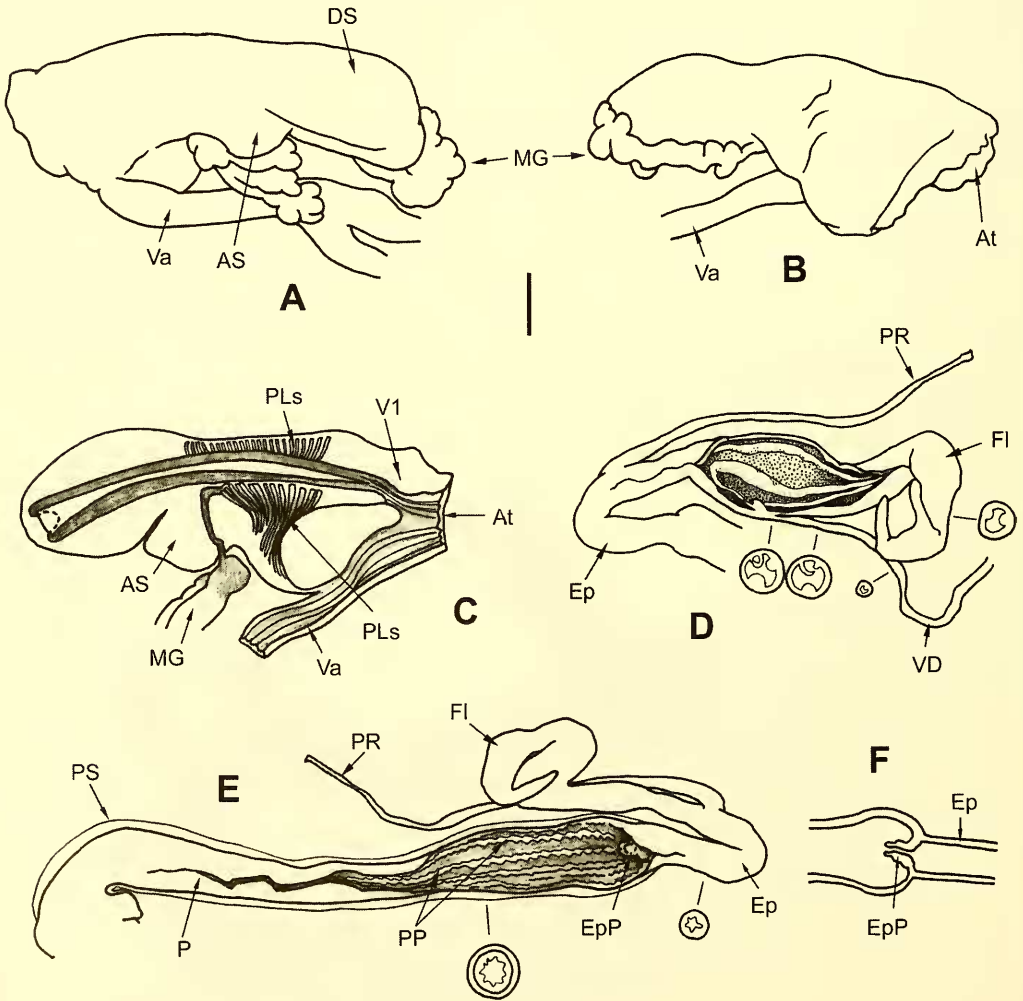


FIG. 13. *Aegista (Aegista) accrescens* (Heude, 1882), IZCAS00027-4. A, B, lateral views of dart sac; C, dart sac, sagittal section; D, flagellum, opened, with cross-sections; E, penial complex, penis opened, with cross-sections; F, section of penis-epiphallus region, diagrammatic. Bar equals 1 mm.

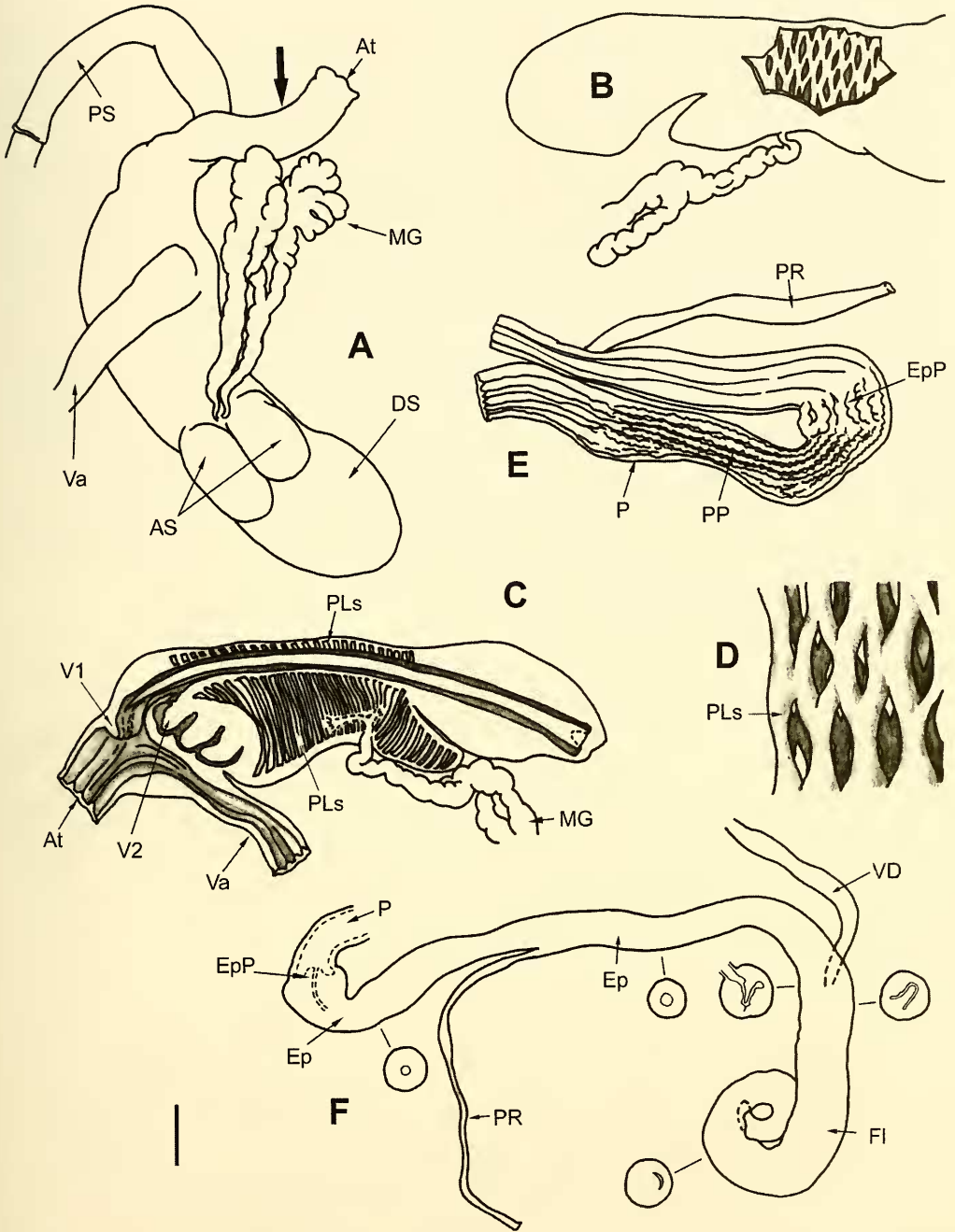


FIG. 14. *Aegista (Plectotropis) gerlachi* (E. Martens, 1881), IZCAS00044-2. A, basal view of dart sac; B, lateral view of dart sac, outer tissue partially removed to show the polylayered structure inside dart sac; C, dart sac, sagittal section; D, polylayered structure in accessory sac, magnified; E, penis and epiphallus, opened; F, penial complex, with cross-sections. Bar equals 1 mm.

2B). Various genera show different patterns of the accessory sac, which has little relationship with its size from external view. The accessory sac is situated usually on the bottom of dart sac, except in *Acusta*, where it is situated near the top of dart sac (Fig. 18B). The structurally simplest accessory sac is an empty sac, only with a few depressed folds (= pilasters) on its inner wall (e.g., Figs. 1B, 7D & 16C).
 Character 15: The accessory sac is bipartite (e.g., Figs. 14A, 22C) or undivided (e.g., Figs. 5A, 7A):

- (0) accessory sac divided into two parts; (1) accessory sac undivided; (2) not applicable because dart sac absent.

Character 16: Presence of V1–V4 in the dart apparatus (= V2 is present):

- (0) V1–V4 indistinct (= V2 is indistinct/absent) (e.g., Figs. 8B, 9B); (1) V1–V4 distinct (= V2 is distinct) (e.g., Figs. 7D, 23E); (2) not applicable because dart sac absent.

Remarks: Inside the dart sac, several valvules (V1–V4) form a tube that contains

one love dart (or two in *Nesiohelix*) serving as mating-related organ (e.g., Figs. 7D, 23E). According to this study, the position and the number of the valvules are intraspecifically stable but vary among the genera studied. The term valvule is used here for the first time in land snail anatomy. It is a small valve-like structure that describes the nature of the chamber boundary (dart sac, accessory sac chamber), visible in sagittal section. However, the position of V1–V4 can easily be determined even when V2 is absent, because: (1) V1 and V4 always form the opening of a muscular tube containing the love dart(s); (2) the space between V4 and V3 is usually the opening of the accessory sac (the only exception is in *Acusta*, in which the accessory sac is situated on the top of dart sac); (3) the space between V3 and V2 is C23, which varies from presence as a pronounced chamber to total absence. Such absence means V2 is lacking morphologically. For this reason, the complexity of the development

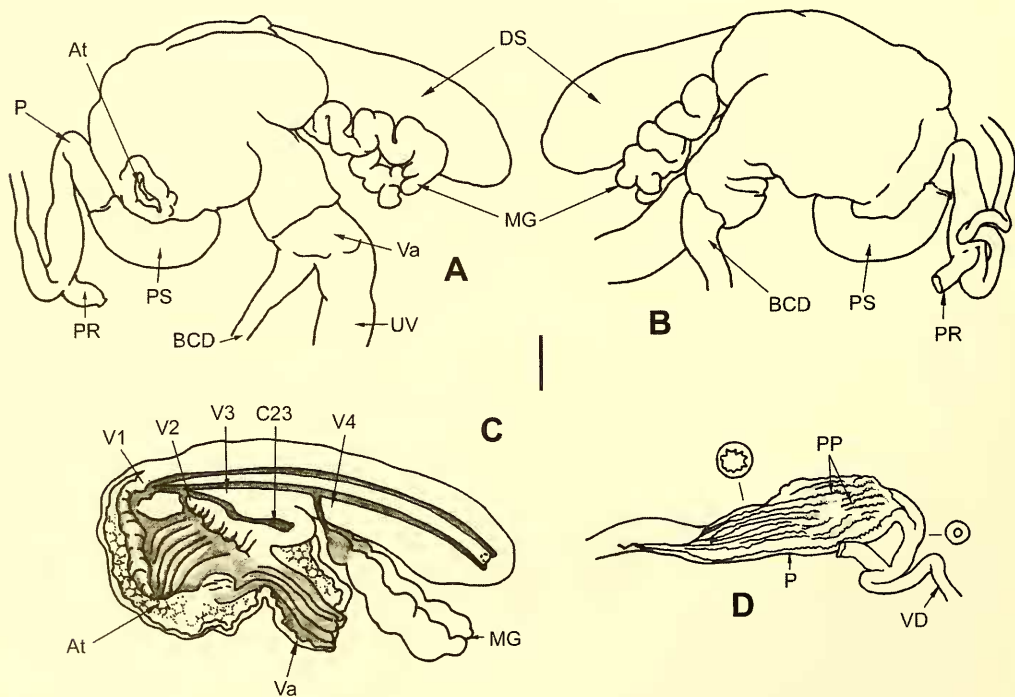


FIG. 15. *Pseudobuliminus (Pseudobuliminus) piligerus* (Möllendorff, 1899), IZCAS00085-21. A, B lateral views of terminal genitalia; C, dart sac, sagittal section; D, penial complex, penis opened, with cross-sections. Bar equals 1 mm.

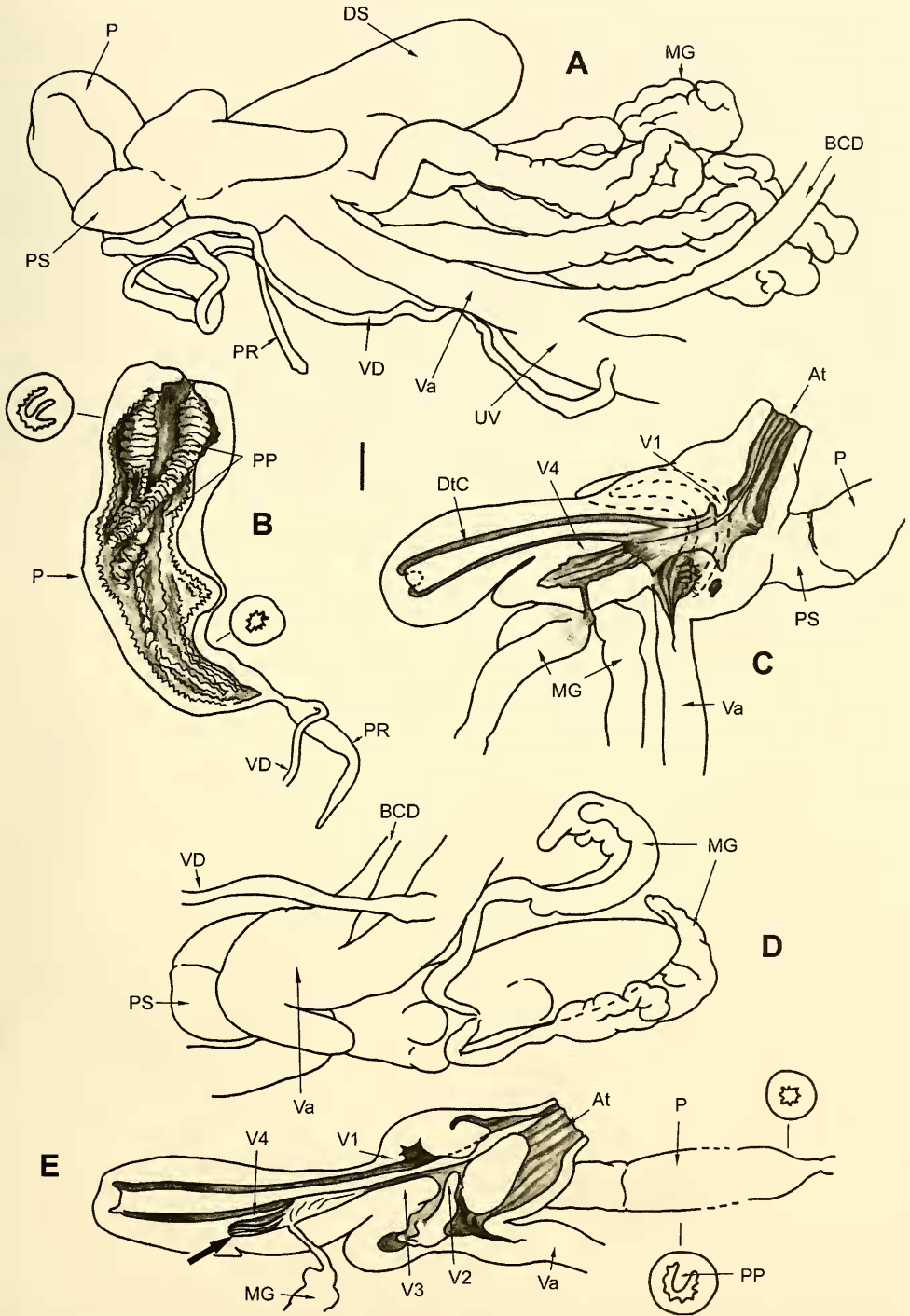


FIG. 16. *Stylpnodiscus*. A, B, C *Stylpnodiscus moellendorffi* Wu, 2001, IZCAS00081-4, Paratype. A, lateral view of terminal genitalia; B, penis, opened, with cross-sections; C, dart sac, sagittal section; D, E *Stylpnodiscus entochilus* Möllendorff, 1899, IZCAS00076-2. D, basal view of dart sac; E, dart sac, sagittal section, in detail, with cross-sections of penis. Bar equals 1 mm.

of the dart sac inner structure is considered, described, and employed for the first time as an important and necessary character for the dart sac in the Bradybaenidae.

Character 17: Presence of a papilla within accessory sac formed by the mucous glands insertion:

(0) without papilla; (1) with a papilla; (2) not applicable because dart sac absent.

Remarks: A papilla with a tiny pore or several tiny pores for the entrance of mucus from mucous glands into the accessory sac is sometimes present. If the mucous gland ducts merge into one common tube, the papilla also has one pore, as in *Acusta ravida* (Fig. 18B, G). When the mucous glands enter the accessory sac separately, two papillae are present, as in *Trishoplita dacostae* (Fig. 19B, indicated by two lower thick solid arrows) or a somewhat complex structure

with numerous pores as in *Nesiohelix swinhoei* and *Euhadra herklotsi* (Figs. 5C, 20D). In most genera, such a structure is absent (other Figs.).

Character 18: Presence of the structure derived from mucous glands entering papilla leading to DtC:

(0) not applicable because mucous glands entrance papilla absent; (1) mucous glands entrance papilla present, its derived part does not lead to DtC; (2) mucous glands entrance papilla present, its derived part leads to DtC (Figs. 19B, 20D, respectively indicated by a upper thick solid arrow).

Character 19: Number of branches of mucous glands:

(0) numerous mucous branches; (1) one spherical mucous gland (Figs. 8, 9); (2) two branches of mucous glands; (3) not applicable because dart sac absent.

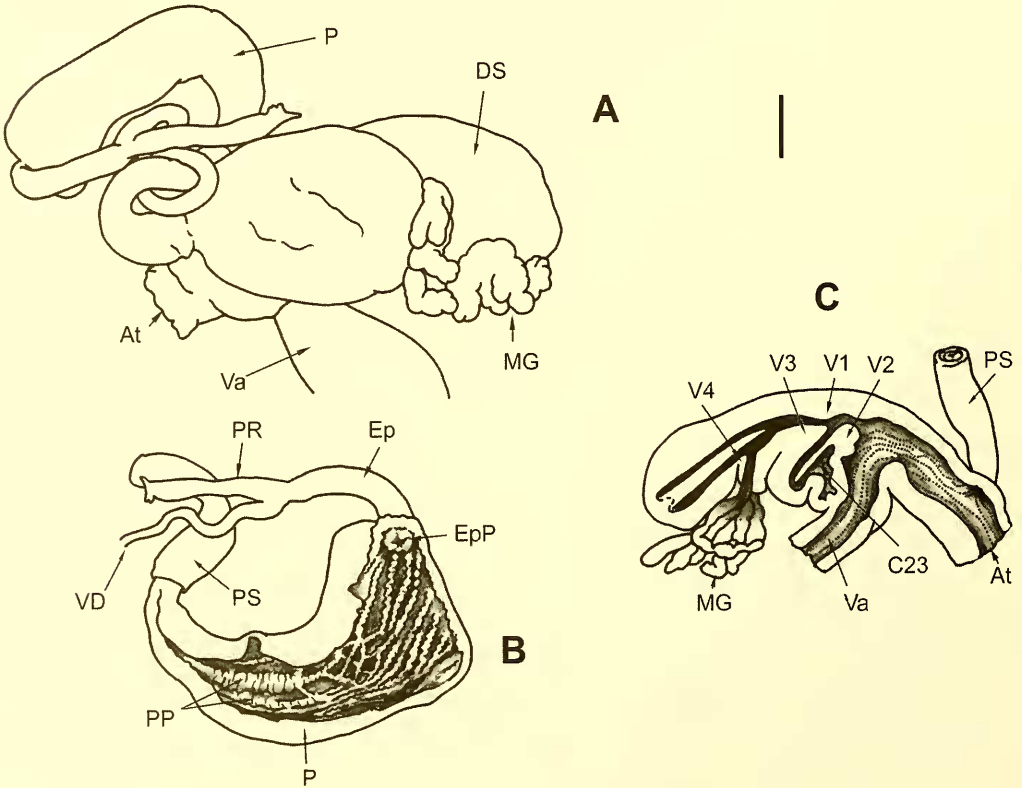


FIG. 17. *Laeocathaica (Laeocathaica) filippina* (Heude, 1882), IZCAS00006. A, B IZCAS00006-5. A, lateral view of terminal genitalia; B, penial complex, penis opened; C, IZCAS00006-6, dart sac, sagittal section. Bar equals 1 mm.

Character 20: The length of vaginal region between dart sac and atrium:

(0) region short; (1) region pronouncedly elongated (e.g., Figs. 9A, 18B); (3) not applicable because dart sac absent.

Character 21: Proximal part of dart sac elongated, forming a neck-structure.

(0) neck-structure absent; (1) neck-structure present (Figs. 3A, 12D); (2) not applicable because dart sac absent.

Character 22: Presence of penis-epiphallus chamber(s):

(0) absent; (1) a simple chamber present

(Fig. 7B, E); (2) more chambers present (Fig. 10D, E).

Remarks: The penis-epiphallus chamber occurs in the wall of penis-epiphallus junction. Dissection shows that there are three cases of differentiation. (1) It is solid (i.e., without any chamber within) between the epiphallic papilla and its wall. (2) There is only a simple chamber between the epiphallic papilla and its wall. (3) As seen in *Helix pomatia* (Helicidae) (Fig. 10D, E), more than one chamber is developed in this area, and some of them extend into the penial wall. All

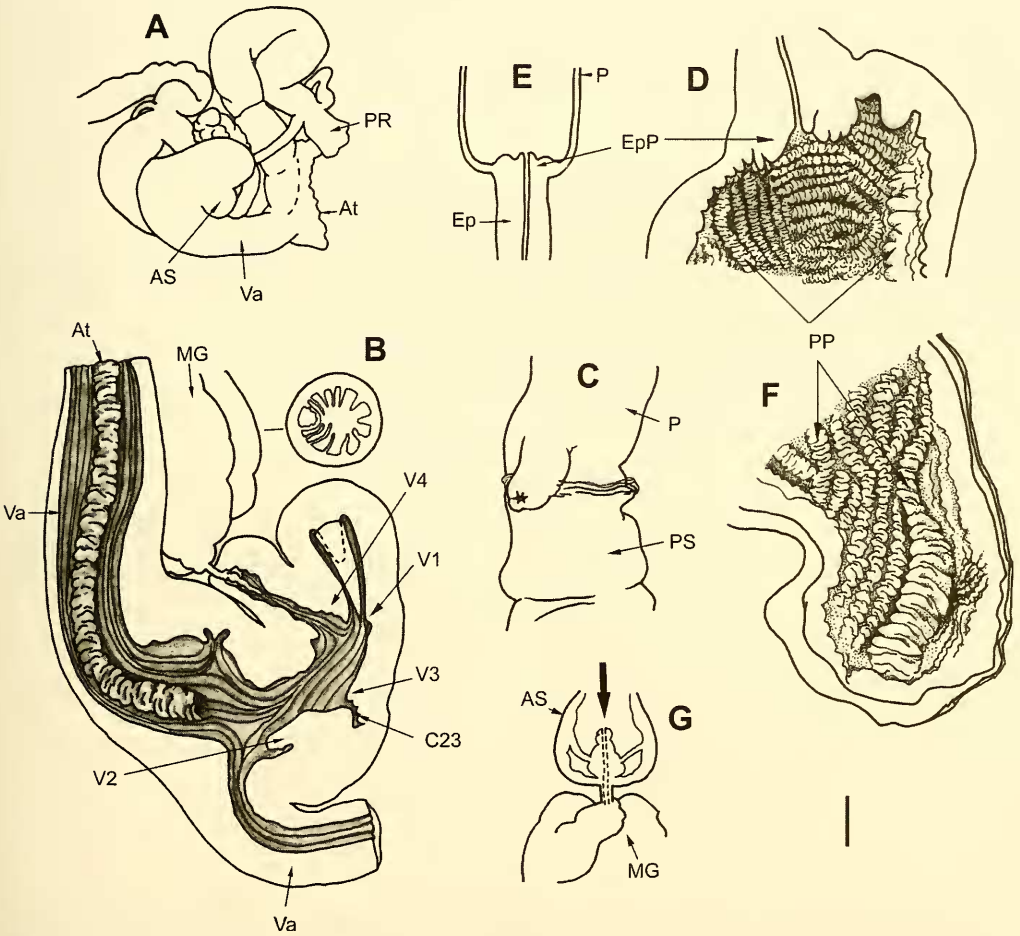


FIG. 18. *Acusta ravidus* (Benson, 1842), IZCAS00944-2. A, general view of genitalia; B, dart sac and part of vagina, sagittal section, with cross-section of vagina; C, region near penial sheath; D, proximal region of penis, opened, showing epiphallic papilla; E, section of penis-epiphallus region, diagrammatic; F, distal region of penis, opened; G, section of accessory sac, papilla of entrance for mucous tubes indicated by a thick solid arrow, diagrammatic. Bar equals 1 mm.

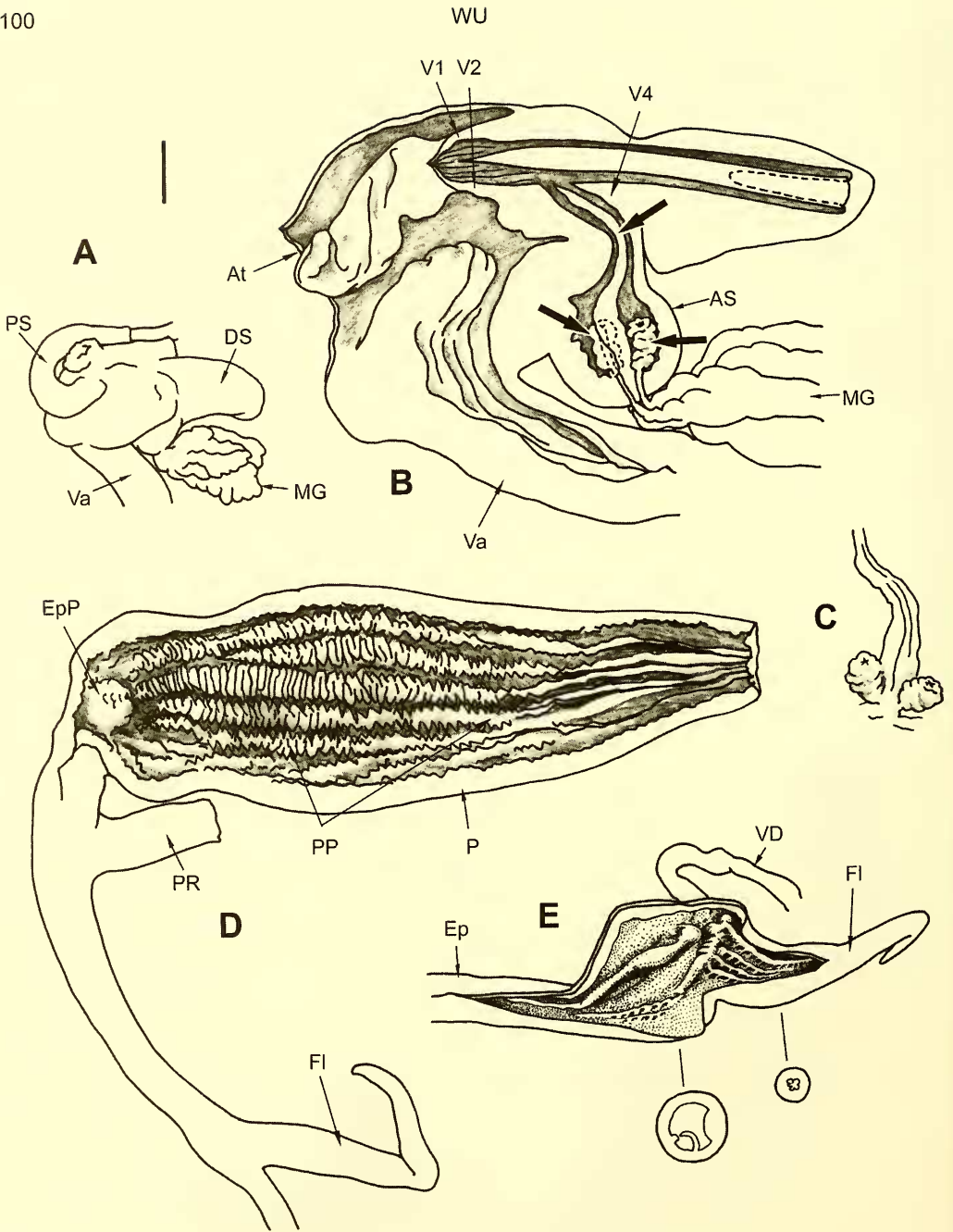


FIG. 19. *Trishoplita dacostae* Gude, 1900. IZCAS00174-2. A, lateral view of dart apparatus; B, dart sac, sagittal section, upper thick solid arrow indicating the structure derived from the mucous glands entering papilla leading to dart chamber, two lower thick solid arrows indicating the mucous glands entering papilla; C, the mucous glands entering papillae and the derived structure; D, penial complex, with penis opened; E, epiphallus and flagellum, opened, with cross-sections. Bar equals 1 mm.

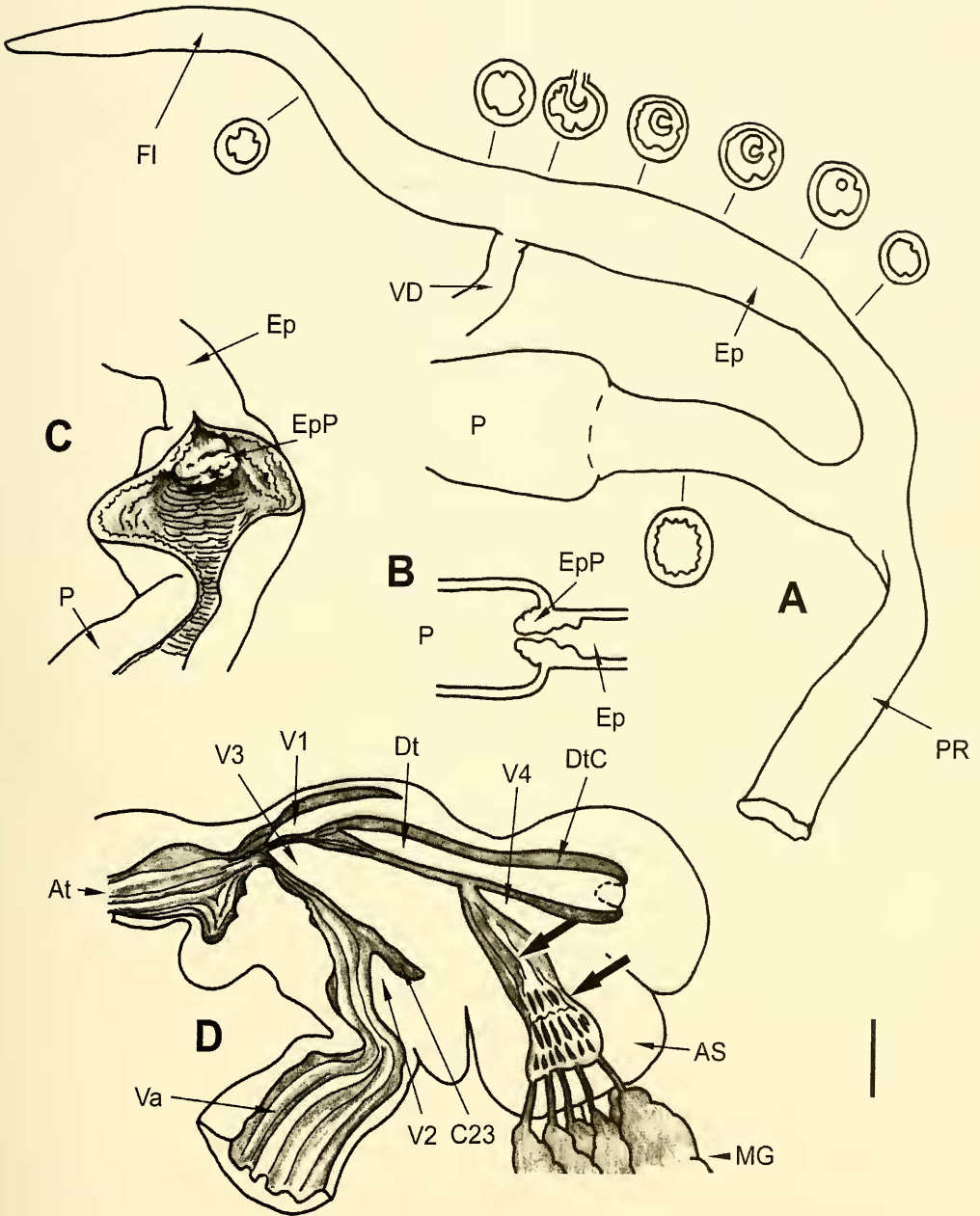


FIG. 20. *Euhadra herklotsi* (E. Martens, 1861), IZCAS01076-1. A, epiphallus and flagellum, with cross-sections; B, section of penis-epiphallus region, diagrammatic; C, penis-epiphallus region, penis opened; D, dart sac, sagittal section, upper thick solid arrow indicating the structure derived from the mucous glands entering papilla leading to dart chamber, lower thick solid arrow indicating the structure of mucous glands entering papilla. Bar equals 1 mm.

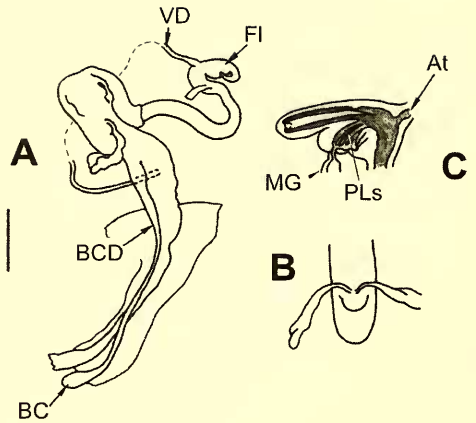


FIG. 21. *Pseudaspasita binodata* (Möllendorff, 1886), IZCAS01075-2. A, general view of terminal genitalia; B, basal view of dart sac, diagrammatic; C, dart sac, sagittal section. Bar equals 1 mm.

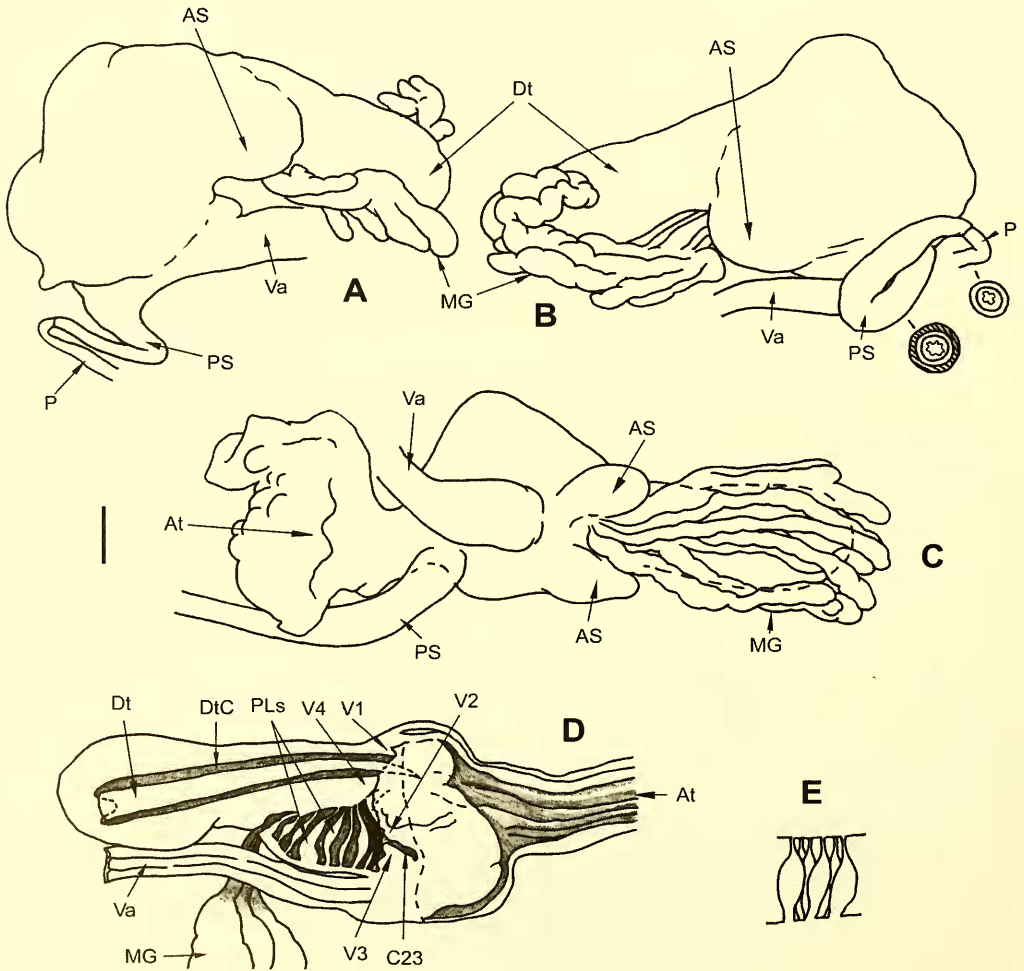


FIG. 22. *Cathaica (Cathaica) fasciola* (Draparnaud, 1801), IZCAS01074-6. A, lateral view of dart sac; B, lateral view of dart sac, with cross-sections of penial sheath and penis; C, basal view of terminal genitalia; D, dart sac, sagittal section; E, poly-layered structure in accessory sac. Bar equals 1 mm.

bradybaenid genera examined, except *Eueuhadra*, n. gen., fall into the first case.

Character 23: Number of darts per dart sac: (0) dart sac containing 1 dart; (1) dart sac containing 2 darts (Fig. 5G, H); (2) not applicable because dart sac absent.

Remarks: In *Nesiohelix swinhoei* (type species of the genus *Nesiohelix*; Richardson, 1983, the type species mistakenly given as *Nesiohelix caspari*; see original introduction of genus by Kuroda & Emura, 1943), the dart sac contains two darts, each of which is wrapped by a muscular tube. These two muscular tubes are attached closely but distinctly divided. In this study, the two darts are the same length rather than "one larger, the other smaller" (Kuroda & Emura, 1943: text-fig. 1), semi-circled in cross-sections, and blunt apically. In some other congeneric species of *Nesiohelix*, such as *N. samarangae* (Kuroda & Miyanaga, 1942) and *N. moreletiana* (Heude, 1882), the dart

sac contains two darts (Habe, 1945, not figured), which is confirmed in this study and is an important synapomorphy characterizing *Nesiohelix*.

Character 24: Internal pilaster of accessory sac differentiated or not:

(0) not differentiated; (1) differentiated (Fig. 1B); (2) not applicable because dart sac absent.

Character 25: Position where the accessory sac is inserted on dart sac:

(0) accessory sac inserted on the bottom of dart sac; (1) accessory sac on the upper side of dart sac (Fig. 18B); (2) not applicable because dart sac absent.

Remarks: The accessory sac is usually situated on the bottom of dart sac, except in *Acusta*, where it is situated at/near the top of dart sac (Fig. 18B, compared to its normal position, e.g., that shown in Fig. 9A). The abnormal position of accessory sac can be observed in all anatomically known

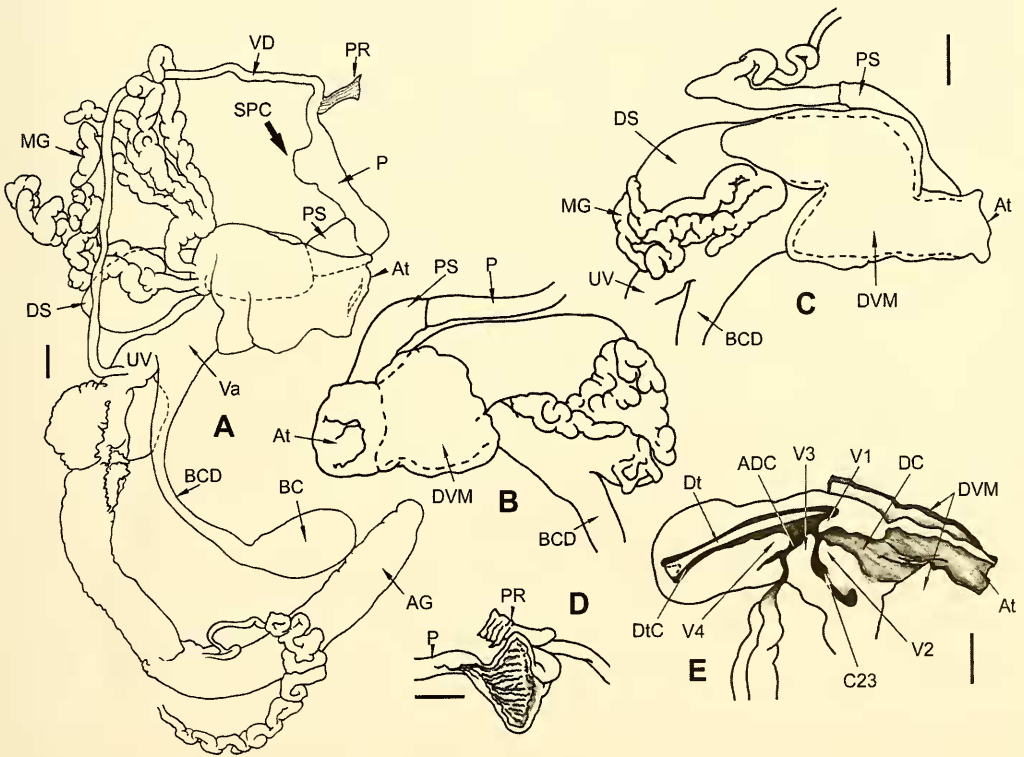


FIG. 23. *Trichobradyla submissa* (Deshayes, 1873), IZCAS00010-3. A, general view of genitalia, simple penial caecum (SPC) indicated by a thick solid arrow; B, C, lateral views of dart sac; D, penis, partially opened; E, dart sac, sagittal section. Bars equal 1 mm (after Wu & Guo, 2003).

Acusta species and is preliminarily considered as the inverse of accessory sac in position (Wu, unpublished paper on *Acusta*).
 Character 26: Presence of sacs inserted on vagina oppsite to dart sac:
 (0) absent; (1) present (Fig. 6A, D, indicated

by thick solid arrows); (2) not applicable because dart sac absent.
 Character 27: Relation of the mantle to the shell.
 (0) shell is not partially enclosed by mantle;
 (1) the mantle partially enclosing shell (observed in *Pfeifferia micans*, SMF323620).

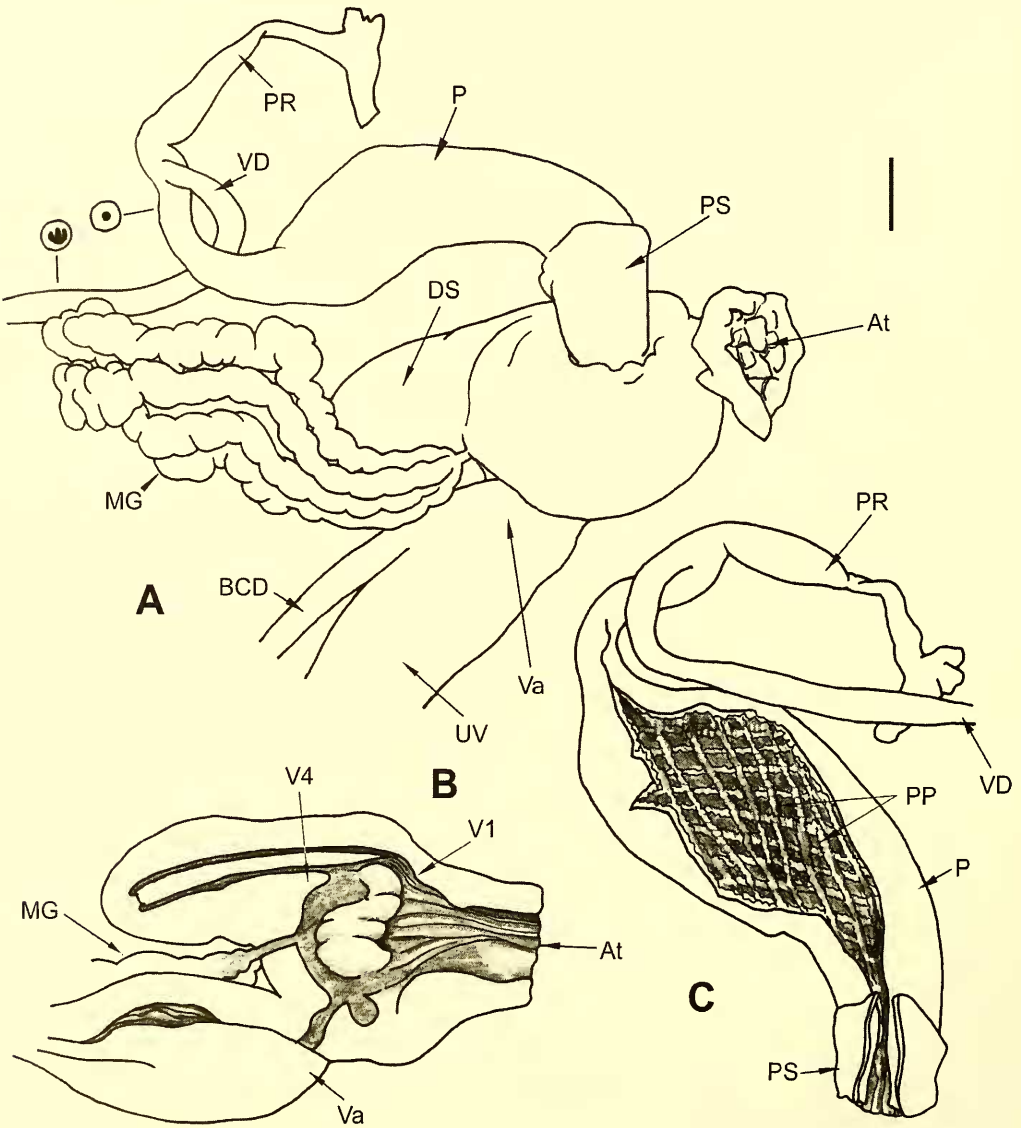


FIG. 24. *Pseudiberus (Platypetasus) chentingensis* Yen, 1935, IZCAS00163. A, lateral view of terminal genitalia, with cross-sections of epiphallus and vas deferens; B, dart sac, sagittal section; C, penial complex, with penis opened. Bar equals 1 mm.

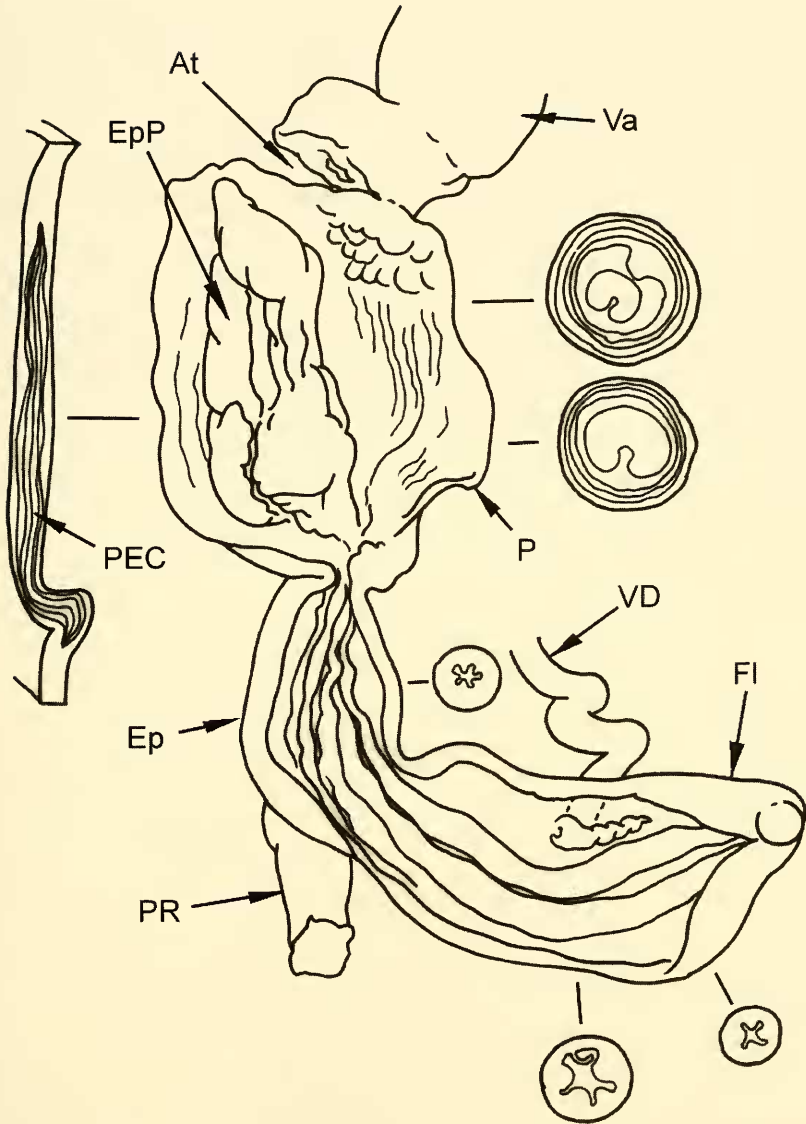


FIG. 25. *Camaena platyodon* (L. Pfeiffer, 1846), IZCAS00833. Male section of terminal genitalia, left, showing saggital section of penial wall; right, showing cross-sections of penis, epiphallus and flagellum.

Cladistic Analysis

The data matrix (Table 1) was submitted to HENNIG86 and Winclada. All the observed apomorphies were included among the char-

acters because they are useful for the characterization of certain terminals, although they are not informative for the construction of the phylogenies. The removal of apomorphies in the analysis will decrease the steps in con-

structuring a cladogram, but will not influence its reliability. Two types of analyses were performed. In the first type of analysis, all characters were weighted equally. Data sets were calculated with an exact algorithm (implicit enumeration). Another type of analysis used the successive weighting function provided by the Hennig86 program, which is considered by Carpenter (1988) to be the best method for weighting characters and choosing among equally parsimonious cladograms. The first analysis produced 11 equally parsimonious trees (EPTs) with length of 96, consistency index (CI) 0.54, and retention index (RI) 0.67. Extended branch swapping was then applied to the initial tree using the branch-breaking

(bb*) command, producing 3,502 bb trees. A strict consensus tree (SCT) (Fig. 26) was then summarized from these 3,502 trees with Winclada in order to find the most unambiguous monophylyes.

In the second analysis, after two iterations of successive approximations weighting and branch-breaking, 87 trees were retained, each with length 274, CI = 0.73, RI = 0.87. The cladograms obtained by the first and the second type of analyses were then introduced to Winclada for rerooting and mapping the distribution of characters. Based on the trees resulting from the second type of analysis, the rooted SCT was produced using Winclada (Fig. 27).

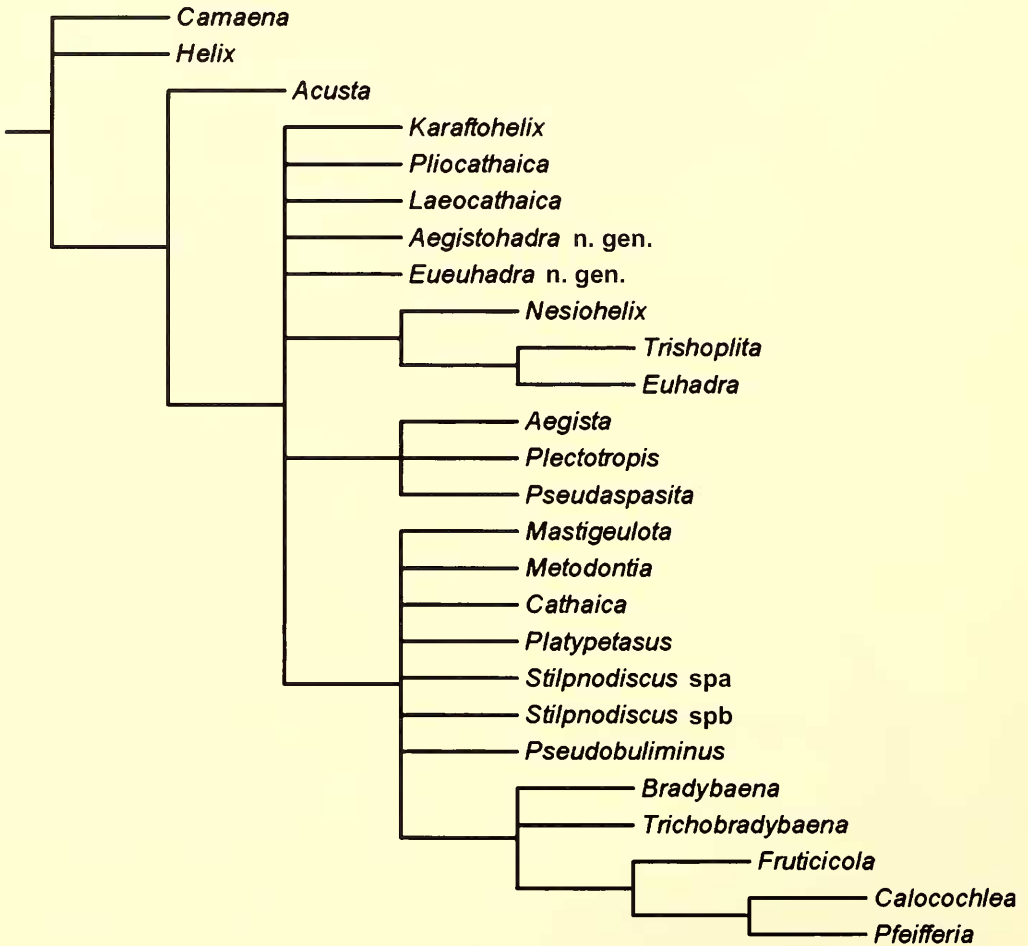


FIG. 26. Rooted SCT resulted from 3,502 EPTs (L = 96, CI = 54, RI = 67) based on equally weighted characters.

In the 3,502 EPTs constructed based on the equally weighted characters, 51 trees were found to be exactly equal respectively, in topology, to those obtained by philosophy of successive approximations weighting. In other

words, 51 out of 87 trees based on weighted characters had the exact topology with the cladograms from the first analysis. When the rooted SCT (Fig. 27) was summarized from the 87 trees from the second analysis, only

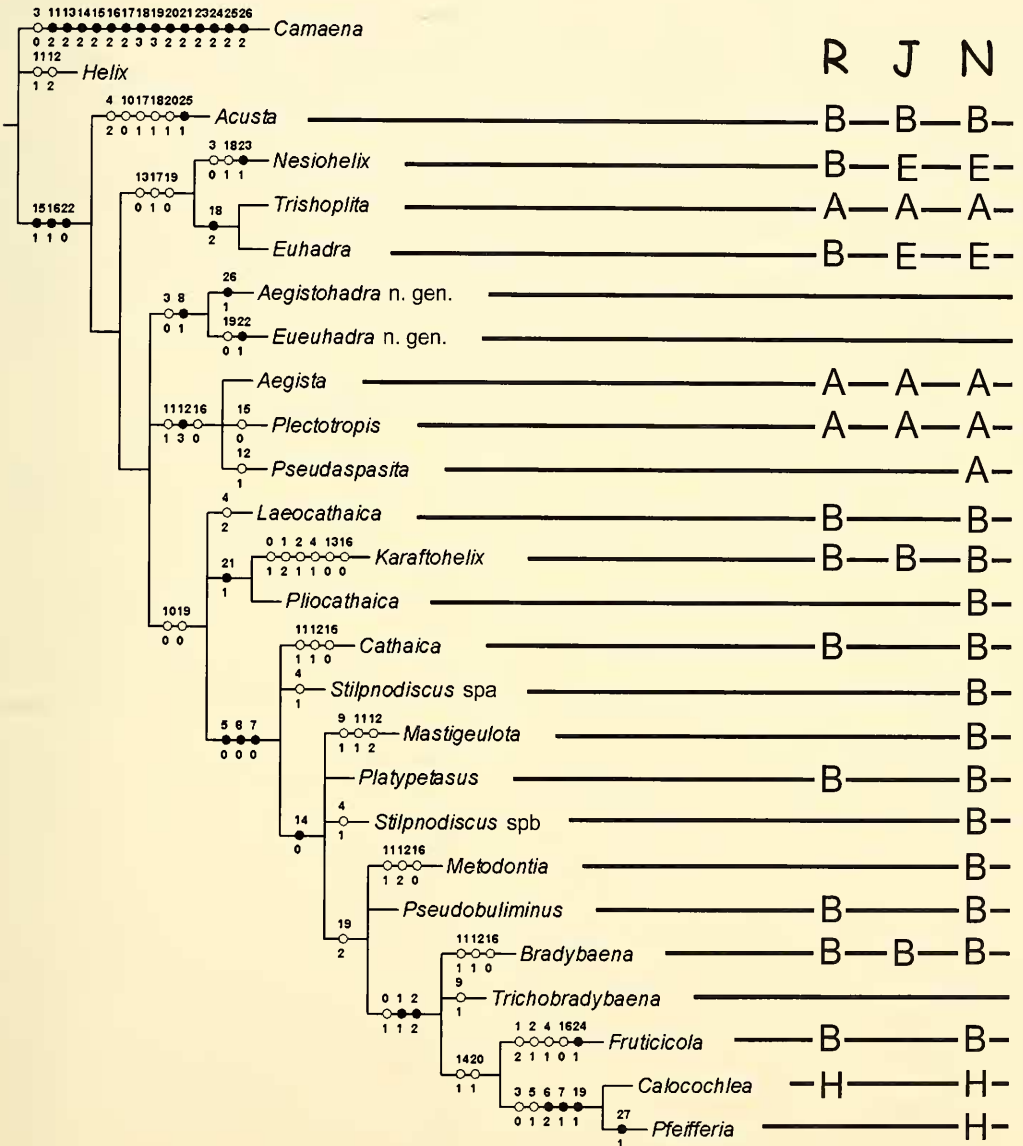


FIG. 27. Left: Rooted SCT resulted from 87 EPTs (L = 274, CI = 73, RI = 87) based on weighted characters, showing the distribution of character states. Solid circle – nonhomoplasious change; empty circle – homoplasious change. Right: Showing suprageneric classification by different authors: A – Aegistinae/Aegistini, B – Bradybaeninae/Bradybaenini, E – Euhadrinae/Euhadrini; H – Helicostylidae/Helicostylinae; R – Russian authors, J – Japanese authors, N – Nordsieck (Nordsieck, 2002).

one node collapsed, so this rooted SCT was thought to be informative and proper for being used both to interpret the present bradybaenid phylogeny and to indicate the reliability of the monophyletic groups.

As shown in the rooted SCT obtained by using the second type of analysis (Fig. 27), the ingroup was well defined by three nonhomoplasious synapomorphies characters 15(1), 16(1), and 22(0) (Fig. 27). Eight clearly distinguished monophylies supported by nonhomoplasious synapomorphy/synapomorphies are as follows:

- (a) The clade (*Trishoplita*, *Euhadra*), was supported by character state 18(2). The monophyly of this clade was also confirmed by the SCT;
- (b) The clade composed of *Aegistohadra* and *Eueuhadra*, supported by character state 8(1);
- (c) The monophyly (*Aegista*, *Plectotropis*, *Pseudaspasita*), supported by character state 12(3). The monophyly of this clade was also confirmed by the SCT;
- (d) The clade composed of *Karaitohelix* and *Pliocathaica*, supported by synapomorphic character state 21(1);
- (e) The clade composed of *Cathaica*, *Stilpnodiscus*, *Mastigeulota*, *Platypetasus*, *Metodontia*, *Pseudobuliminus*, *Bradybaena*, *Trichobradyaena*, *Fruticicola*, *Calocochlea*, and *Pfeifferia*, supported by synapomorphic character states 5(0), 6(0) and 7(0);
- (f) The clade embedded in (e), *Mastigeulota*, *Platypetasus*, *Stilpnodiscus* spb, *Metodontia*, *Pseudobuliminus*, *Bradybaena*, *Trichobradyaena*, *Fruticicola*, *Calocochlea*, and *Pfeifferia*, supported by synapomorphic character state 14(0). The monophyly of this clade was also confirmed by the SCT;
- (g) The clade composed by *Bradybaena*, *Trichobradyaena*, *Fruticicola*, *Calocochlea*, and *Pfeifferia*, supported by synapomorphic character states 1(1) and 2(2). The monophyly of this clade was also confirmed by the SCT;
- (h) The clade *Calocochlea* and *Pfeifferia*, supported by synapomorphic character states 6(2), 7(1), and 19(1). The monophyly of this clade was also confirmed by the SCT.

Based on the characters extracted from terminal genitalia, only part of the examined bradybaenid genera could be characterized by their autapomorphies. The terminal taxa

Trishoplita, *Euhadra*, *Aegista*, *Pliocathaica*, *Calocochlea*, *Pseudobuliminus*, and *Platypetasus* had the opposite situation, that is, considering the anatomy of terminal genitalia, they were not characterized by derived characters. As indicated in Figure 27, they seemed to be defined by the "loss of character state(s)" rather than autapomorphies that could be directly observed.

DISCUSSION

The proposed phylogeny of bradybaenid genera has almost no similarity with the previous systems reviewed by Nordsieck (2002). Previously, knowledge of bradybaenid systematics came from the shell and very few genital features, and resulted from methodologically subjective analyses. The present cladograms, with too many branches, are not strongly supported, indicating that this is a preliminary result, providing a testable hypothesis of relationships among bradybaenid genera. The hypothesis reflected by the cladogram in Figure 27 is preferred, because it represents the best testable systematic hypothesis explaining the present data set.

While the hypothesis presented is limited and requires the addition of data from many unstudied taxa, focus on some monophyletic branches with relatively strong support shows convincing results. The monophyletic clade of *Calocochlea* and *Pfeifferia*, representatives of the Helicostyliinae Ihering, 1909, is well nested in the ingroup, suggesting that Helicostyliinae are a bradybaenid group rather than a separate family (Helicostylidae *sensu* Schileyko, 1991). In the definition of the family Helicostylidae *sensu* Schileyko (Schileyko, 1991: 221), "the flagellum is variously developed but is always present" is a dubious character, because the present work shows that both *Pfeifferia micans* (type species of *Pfeifferia*) and *Calocochlea coccomelos* have no flagellum (Figs. 8, 9).

The present phylogeny, by artificially excluding helicostyliine groups, is more or less compatible with the tripartite plan of bradybaenid genera, that is, tripartite classification of (1) modified Aegistini (= subfamily Aegistinae *sensu* Kuroda & Habe, 1949, listed as a tribe by Nordsieck, 2002; partial Aegistinae *sensu* Schileyko, 1991), (2) Euhadrini (= Euhadrinae Minato, 1988, listed as a tribe by Nordsieck, 2002: including both *Nesiohelix* and *Euhadra*),

and (3) Bradybaenini (= Bradybaeninae *sensu* Kuroda & Habe, 1949, listed as a tribe by Nordsieck, 2002) (Fig. 27). The Aegistini was distinguished from Bradybaenini by the presence of the flagellum. The present phylogenetic hypothesis suggests the flagellum has been at least convergently lost in Bradybaenidae twice (Fig. 27). Accordingly, this character should not be employed as the proper character defining Aegistinae as used in the original designation (Kuroda & Habe, 1949). The present hypothesis shows the reliability for the monophyly of (*Trishoplita*, *Euhadra*), which are distributed in both Aegistini (including genus *Tishoplita*: Kuroda & Habe, 1949; Minato, 1988; Schileyko, 1991; Nordsieck, 2002) and Euhadrini. Therefore, Aegistini should be considered a paraphyletic group as indicated by the evidence that *Trishoplita* is embedded in the clade of Euhadrini.

As clearly indicated by the all ETPs (3,502 ETPs, not figured) from the first analysis and cladogram based on the weighted characters (in all 87 ETPs, not figured), *Acusta* occurred most basally in the cladograms. Also indicated by the rooted SCTs (Figs. 26, 27), *Acusta*, which was placed in the Bradybaenini (= Bradybaeninae *sensu* Russian and Japanese authors), was confirmed as the sister group to all the remaining bradybaenids examined. Thus, the Bradybaeninae is a paraphyletic group, and *Acusta* should not be placed in Bradybaenini (*sensu* Nordsieck, 2002). In summary, the result obtained demonstrates the Bradybaenini (*sensu* Nordsieck, 2002) is not monophyletic.

Cathaica was divided into several subgenera by Andreae (1911) based on shell characters. This study examined two of them, *Cathaica* (*s. str.*) and *Cathaica* (*Pliocathaica*). The results here show that *Cathaica* (*s. str.*) has a much closer relationship to the terminals in Clade (e), than to *Pliocathaica*, which is closest to *Karatohelix* (Fig. 27). Accordingly, subgroups of *Cathaica* may be polyphyletic.

Some characters used by other authors are thought to be unreliable after careful dissections and thus are omitted from the present study. The widening of the basal bursa copulatrix duct, which was used by Schileyko (1991) as a diagnostic character of Bradybaenidae *sensu* Schileyko, is not included in the present data set, because this part varies in thickness according to physiological state, for example in *Aegista accrescens* (Heude,

1882), as observed by the author. Some characters once used to describe the genitalia are ambiguous and thus should be avoided being used. For example, the development status of the accessory sac, which is an autapomorphy in the diagnostic definition for Helicostylidae (*sensu* Schileyko, 1991) as "an accessory sac is weakly developed or lacking", seems not to be so definite and consequently is less informative or misleading. In the Bradybaeninae (*sensu* Nordsieck, 2002), the accessory sac shows a variety of development states, such as size range, differentiation of the internal pilasters, and occurrence of the mucous glands entering papilla. Therefore, the accessory sac comprises a series of characters instead of a character with several character states. In Helicostyliinae (= Helicostylidae *sensu* Schileyko, 1991), the genera *Calocochlea* and *Pfeifferia* (Figs. 8B, 9B) have an accessory sac with similar structure as those seen in the bradybaenine, for example, in *Trichobradysbaena* (Fig. 23E) and in *Pliocathaica* (Fig. 12D). This suggests some characters, such as seen in the non-homoplasious characters (both synapomorphies and autapomorphies) in this study, should be given special attention as to whether they are shared by or transformed into certain states in any other bradybaenid genus not covered in this work. Careful consideration of this problem will enhance the reliability of the phylogeny obtained.

Cuezzo (1998) points out that there are three different problems seen in the published literature of the Xanthonychidae (= Helminthoglyptidae). I see the same problems in the current the study of the Bradybaenidae. Virtually in all the published literature, the systematics of Bradybaenidae is established on "arbitrary narrative character transformations". Any effort to make a predictive classification of the Bradybaenidae (or any other group), as Nordsieck (2002) suggests, should be based on testable hypotheses, and after as many species as possible are examined. The present work does not aim to provide a definitive classification of the Bradybaenidae, as many genera and many other important characters, for example, anatomical (besides terminal genitalia), molecular, and chromosomal, are not included in the data set. However, it does suggest that the phylogeny of the Bradybaenidae is complex and considerable further work on the systematics for this group is needed.

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- APPENDIX I: Taxa studied
- Acusta ravida* (Benson, 1842), type species of the genus: IZCAS00944, Jiangning County, Jiangsu Province, coll. unknown. Four adult specimens (two dissected) and two young specimens.
- Aegista (Aegista) accrescens* (Heude, 1882): IZCAS00027, Xiushan County (28.4°N, 108.9°E), Sichuan Province, 1986-VII-21, coll. De-Niu Chen & Jia-Xiang Gao. Six adult specimens (three dissected).
- Aegista (Plectotropis) gertlachi* (E. Martens, 1881): IZCAS00044, Guangdong Province, other collection data unknown. Nine adult (two dissected) and three young specimens.
- Bradybaena similis* (Rang, 1831) (not A. Férussac 1821; see Nordsieck, 2002), type species of the genus: IZCAS01072, Fuzhou, Fujian Province, 1975-X-16, coll. unknown. Forty adult (two dissected) and 17 young specimens.
- Cathaica (Cathaica) fasciola* (Draparnaud, 1801), type species of the genus: IZCAS01074, Pi County, Xuzhou, Jiangsu Province, 2000-V-2, coll. Qi-Lian Qin. Numerous specimens (three dissected).
- Cathaica (Pliocathaica) gansuica* (Möllendorff, 1899): IZCAS00210, Dachuanxiang, Zhouqu County, Gansu Province, 1200 m alt., 1998-V-9, coll. De-niu Chen & Guo-Qing Zhang. 166 specimens (two dissected).
- Fruticicola fruticum* (O. F. Müller, 1774), type species of the genus: IZCAS01009, limestone quarry near Klodzko, Wapniarka Mt., Lower Silesia, Poland, 1999-VI-26, coll. Min Wu & Andrzej Wiktor. Seven adult specimens (two dissected) and one young specimen.
- Karafftohelix weyrichii* (Schrenck, 1867): IZCAS01080, near Yushno-Sakhalinsk City, Sakhalin Island, Russia, 2001-VII-29, coll. Larisa A. Prozorova. One adult (dissected) and four young specimens.
- Mastigeulota kiangsinensis* (E. Martens, 1875), type species of the genus: IZCAS00003, Huangnipo, Badong County (31.0°N, 110.3°E), Hubei Province, coll. De-Niu Chen, 1984-VI-29. Six adult (two dissected) and one young specimen.
- Metodontia yantaiensis* (Crosse & Debeaux, 1863): IZCAS00131, Quyang County, Hubei Province, coll. Min Wu. Fifteen adult specimens (two dissected) and 19 young specimens.

- Pseudaspasita binodata* (Möllendorff, 1886), type species of the genus: IZCAS01075, Beiquan Park, Beipei, Chongqin, 1964-V-12. Twenty-seven adults (two dissected) and 12 young specimens.
- Pseudiberus (Platypetasus) chentingensis* Yen, 1935: IZCAS00163, Jiaozuo, Henan Province, 1999-VII-22, coll. Guang-Wen Chen. Six adults (two dissected) and 17 young specimens.
- Stilpnodiscus moellendorffi* Wu, 2001: IZCAS00081, type specimens, Shanggou, Shawanxiang, Dangchang County, Gansu Province, 1998-VI-6, coll. De-Niu Chen & Guo-Qing Zhang.
- Stilpnodiscus entochilus* Möllendorff, 1899: IZCAS00076, Guoyuanxiang, Nanping County (now Jiuzhaigou County) (33.2°N, 104.2°E), Sichuan Province, 1000 m alt., coll. De-Niu Chen & Guo-Qing Zhang, 1998-V-18. 25 adult (four dissected) and 17 young specimens.
- Laeocathaica (Laeocathaica) subsimilis* (Deshayes, 1873): IZCAS00006, Xingjianxiang, Nanchong (30.8°N, 106.1°E), Sichuan Province, coll. unknown, 1964-V-20. Eleven adult specimens (four dissected).
- Pseudobuliminus (Pseudobuliminus) piligerus* (Möllendorff, 1899): IZCAS00085, Anchanghexiang, Wen County (33.0°N, 104.6°E), Gansu Province, 1200 alt., coll. De-Niu Chen & Guo-Qing Zhang, 1998-V-19. 287 specimens (three dissected).
- Trishoplita dacostae* Gude, 1900: IZCAS00174, Kobayashi Hiyazaki, Japan, coll. unknown, 1998-X. Six adult (three dissected) and six young specimens.
- Euhadra herklotsi* (E. Martens, 1861): IZCAS01076, Ishigakijima, 1931-VII, coll. Shikanu (?). Two adult specimens (one dissected).
- Nesiohelix swinhoi* (L. Pfeiffer, 1865), type species of the genus (in Richardson, 1983, the type species mistakenly given as *Nesiohelix caspari*; Kuroda & Emura, 1943): IZCAS00055, Yilan County (24.7°N, 121.7°E), Taiwan Province, coll. unknown, 1896-X. Two adult specimens dissected.
- Aegistohadra delavayana* (Heude 1885) n. gen. and comb.: IZCAS00132, Zhibenshan Mt., Baoshan (26.3°N, 104.4°E), Yunnan Province, coll. De-Niu Chen, 1981-VI-23. Four adult specimens (two dissected) and three young specimens. Paratypes, IZCAS-type-2902-1 and IZCAS-type-2902-2, Fa Kouan Tchen, coll. Unknown.
- Aegistohadra seraphinica* (Heude, 1889): paratypes, IZCAS-type-3071-1 and IZCAS-type-3071-2, Si-lin, Guangxi, coll. Unknown.
- Eueuhadra gonggashanensis*, n. gen. & sp., type species of the genus: IZCAS00067, west slope of Gonggashan Mt., Kangding County (30.0°N, 101.9°E), Sichuan Province; coll. De-Niu Chen & Jia-Xiang Gao, 1982-IX-9. Fifteen adult (four dissected) and seven young specimens; IZCAS01061, border of Jiuzhaigou County and Songpan County (33°02'14.4"N, 103°42'32.1"E), Sichuan Province, coll. Min Wu. One adult specimen dissected.
- Trichobradyla submissa* (Deshayes, 1873), type species of the genus: IZCAS00010, Hanzhong, Shaanxi Province, 1992-IV-15, coll. De-Niu Chen. Numerous specimens (three dissected).
- Helix pomatia* (Linné, 1758) (Helicidae), type species of the genus: IZCAS00188, limestone quarry near Klodzko, Wapniarka Mt., Lower Silesia, Poland, 1999-VI-26, coll. Min Wu & Andrzej Wiktor. One adult specimen dissected.
- Calocochlea coccomelos* (Sowerby, 1840): SMF323619, Philippines: Sibuyan, ex Möllendorff. One specimen dissected.
- Pfeifferia micans* Pfeiffer, 1845, type species of the genus: SMF323620, Philippines: Cagayan, Pamplona, O. v. Möllendorff. One adult specimen dissected.
- Camaena platyodon* (L. Pfeiffer, 1846) (Camaenidae): IZCAS00833, Hainan, other collection data lacking. Eleven adult (three dissected) and one young specimens.

APPENDIX II: New taxa

Aegistohadra, n. gen.

Type species: *Nanina delavayana* Heude, 1885: 102, pl. xxvi, fig. 8.

Aegistohadra delavayana (Heude, 1885), n. gen. & comb.

(Figs. 6, 28–31; Table 2)

Material

Four adults (IZCAS00132-1–4) of which two are full grown but broken and three young shells were examined, Zhibenshan Mt., Baoshan (26.3°N, 104.4°E) ("Yunlong County" in original label is a printing error), Yunnan Province; coll. De-Niu Chen, 1981-VI-23.

TABLE 2. Conchological measurements and counts of specimens IZCAS00132, *Aegistofhadra delavayana* n. gen. & comb.

	Shell height	Shell width	No. whorls	No. proto-conch whorls	Apertural length	Apertural width	Umbilicus diameter	Height/width	Umbilicus diameter/shell width
IZCAS00132-1	16.39	29.10	4 ⁷ / ₈	1 ³ / ₈	12.81	12.87	4.73	0.56	0.16
IZCAS00132-2	20.98	-	5 ³ / ₈	1 ³ / ₈	15.41	15.96	-	-	-
IZCAS00132-3	20.13	32.14	5 ³ / ₈	1 ³ / ₈	-	-	6.37	0.63	0.20
IZCAS00132-4	21.27	-	5 ¹ / ₄	1 ³ / ₈	17.03	16.58	6.32	-	-

Two paratype specimens of *Nanina delavayana* H., IZCAS-type-2902-1 and IZCAS-type-2902-2 (Fig. 32), Fa Kouan Tchen, coll. unknown. Two paratype specimens of *Helix seraphinica* Heude, 1889 (Fig. 33).

Etymology

The genus name is derived from the names of two bradybaenid genera *Aegista* and *Euhadra*.

Diagnosis

Female part of genitalia with sac-shaped structure on vagina opposite to dart sac.

Short Description

Shell strongly depressed, sinistral, thick and solid. Umbilicus broad. Protoconch with radial wrinkles. Penial sheath absent; penis with a penial caecum near penial retractor; epiphallus with a flagellum; penis-epiphallus chamber absent; accessory sac undivided; in dart apparatus polylayered structure absent; V1-V4 in the dart apparatus present; two sacs inserted on vagina opposite to dart sac.

Full Description

Shell sinistral, thin but solid. Apex distinct. Whorls convex. Suture strongly impressed. Umbilicus narrow to moderately wide. Columella oblique; columellar lip dilated, slightly covering umbilicus. Adult shell and young shell with smooth surface, spiral furrows irregularly and sparsely present, ribs absent; growth lines not accompanied by irregular thickenings, background microscopic ripples absent. Protoconch with radial wrinkles. Immature shells unkeeled and unangulated. Body whorl large, unkeeled, weakly descending in front, with convex bottom. Aperture rounded, oblique. Lip toothless, equally expanded, thin within. Peristome reflexed equally. Parietal callus indistinct. Shell dull, opaque; yellowish brown with two brown bands, one above and one beneath periphery, the lower sometimes not as distinct as the upper. Bottom of body whorl yellowish brown (Figs. 29, 30).

Animal uniformly gray. Jaw arcuate with 7–8 ribs dentating the concave margin, ribs contiguous, wide. In a paratype (IZCAS00132-2), radula with 169 rows of teeth, each with one



FIG. 28. Distribution map. Square: *Aegistohadra delavayana* n. gen. & comb.; dots: *Eueuhadra gonggashanensis* n. gen. & sp.

central tooth and 53 lateral teeth at each side; central tooth and lateral teeth L_1 – L_{19} unicuspid; L_{20} – L_{53} each with an endocone and an ectocone (Fig. 31E).

Genitalia: Penial sheath absent (Figs. 6A, 31A), except for some basal connective tissue present near atrium covering penis. Penis short, slender, with a finger-shaped penial caecum near penial retractor (Figs. 6A, 6C, 31A, 31B). Retractor simple, thin or thick, short

or in moderate length. Epiphallus thick, short, with more or less protruding symmetrical epiphallic papilla (Figs. 6C, 31C). Penis-epiphallus chamber absent. Flagellum roundly blunt at end, with fairly smooth surface, thick, short (Figs. 6A, 6C, 31A, 31B); innerly folds not forming a C-shaped open tube towards flagellum or epiphallus (Figs. 6C). Pore of penial papilla located near the pore leading to penial caecum, mainly built by two pilasters derived from four thicker ones longitudinally arranged along penial inner wall (Figs. 6C, 31C). Dart sac developed, with an accessory sac below. Accessory sac large in size, slightly elongated (Figs. 6A, 6D, 31A). Dart sac containing one dart. Dart about 7.0 mm in length, almost straight, slightly expanding basally; cross section of dart throughout rounded or ovate at lower part, upper 1/4 with 2 opposite sharp ridges. (Fig. 31F). Inside dart sac, ADC sharing same entrance with DtC; V1–V4 present, V2 merged into a pilaster towards vagina; V1, V3 and V4 forming DtC; C23 present, but opened to vagina (Fig. 6D). Two sacs on vagina opposite dart apparatus, one with two highly ridged pilasters, and another just beneath the first one and with connective tissue inside, of unknown function (Figs. 6A, B & D); DVM absent. Mucous glands with two lobules, each as long as dart sac, stalks distinct, separated from dart sac and tied tightly to the trunk of vagina, inserting near base of dart sac (Fig. 31A). Lobules simply branched, distally sac-shaped. Bursa copulatrix slightly elongated,

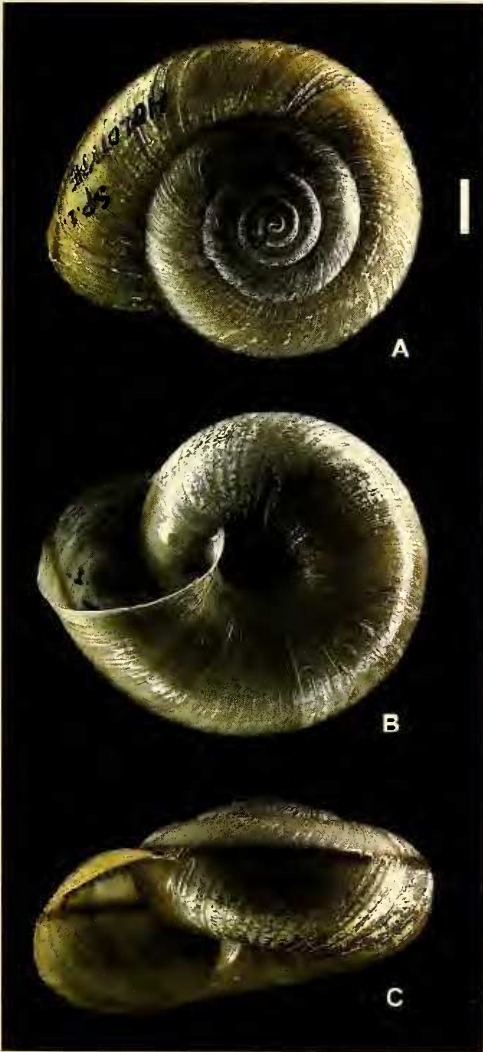


FIG. 29. *Aegistohadra delavayana* n. gen. & comb., shell near mature, IZCAS00132-1. A, apical view; B, basal view; C, apertural view. Bar equals 5 mm.



FIG. 30. *Aegistohadra delavayana* (Heude, 1885), n. gen. & comb., shell, IZCAS00132-3. A broken but adult shell, showing aperture structure. Bar equals 5 mm.

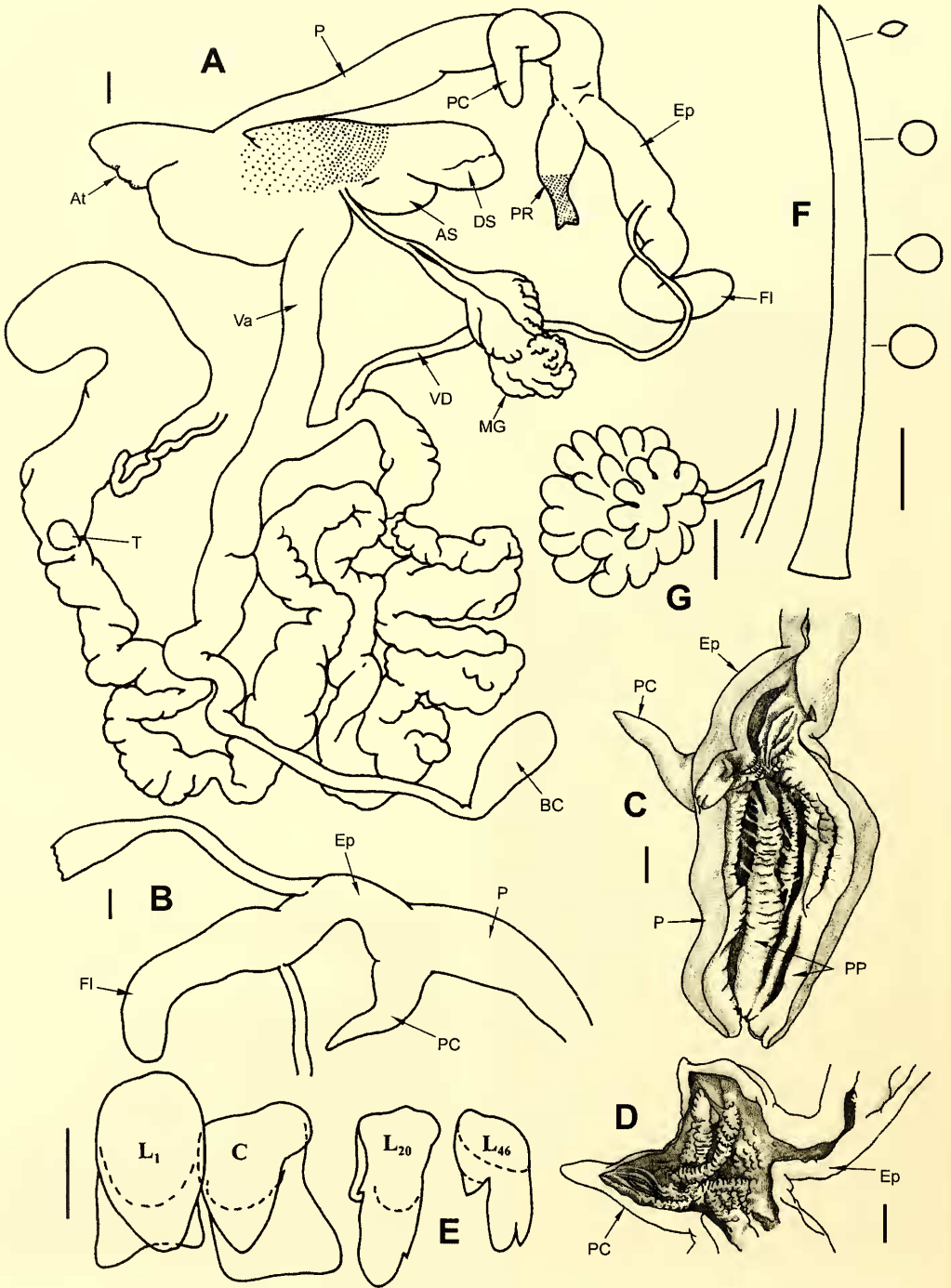


FIG. 31. *Aegistohadra delavayana* (Heude, 1885), n. gen. & comb., IZCAS00132-2. A, general view of genitalia; B, penial complex; C, penis and epiphallus, opened; D, penial caecum (PC), opened; E, teeth of radula, bar equals 25 μ m; F, dart, with cross-sections; G, a leaf of ovotestis. A-D, F, G, bars equal 1 mm.

well differentiated from its duct (Fig. 31A). Bursa copulatrix duct moderately long, inserting low on vagina (Fig. 31A). Ototestis palm-shaped, with single stalk (Fig. 31G). Holotype: dart sac 10.0 mm in length, 2.5 mm in width, ratio of width to length 0.3; mucous duct length 9.3 mm; vagina length 13.8 mm; bursa

copulatrix duct 18.0 mm long, basal width 1.3 mm; transverse diameter (maj.) of bursa copulatrix 1.8 mm, sagittal diameter (maj.) of bursa copulatrix 3.5 mm; vas deferens length 16.3 mm; penis length 12.0 mm; flagellum length 5.8 mm; epiphallus 3.8 mm in length; penial retractor 3.8 mm long (Fig. 31G).

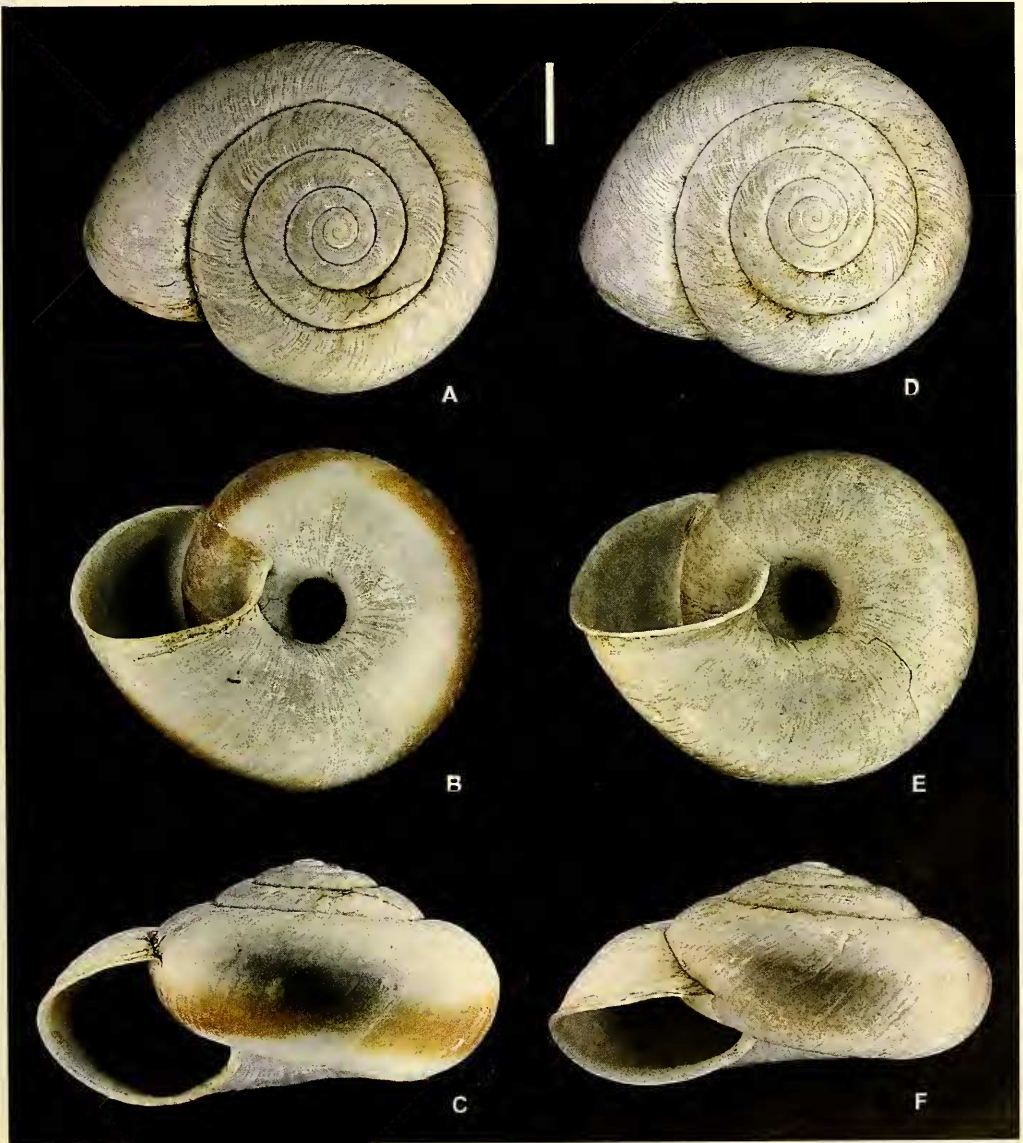


FIG. 32. *Aegistohadra delavayana* (Heude, 1885), n. gen. & comb., shell, paratypes, A-C, IZCAS-type-2902-1; D-F, IZCAS-type-2902-2. Bar equals 10 mm.

Range

Southwestern China (Fig. 28).

Remarks

This species can be distinguished from all known bradybaenid species in that the female part of the genitalia has a sac-shaped structure on the vagina opposite to the dart sac. It also differs from all bradybaenids, except

Eueuhadra gonggashanensis, n. gen. & sp., in having a pronounced penial caecum.

Based on shell features, although distinctly larger (diam. maj.: 55 mm; min.: 48 mm; alt.: 30 mm), it is possible that *Helix seraphinica* Heude, 1889, from Silin (as "Xilin" in today's spelling, Guangxi Province) should be placed in *Aegistohadra* because of their similar shell shape (Fig. 33), as suggested by H. Nordsieck



FIG. 33. *Helix seraphinica* Heude, 1889, shell, paratypes, A-C, IZCAS-type-3071-1; D-F, IZCAS-type-3071-2. Bars equal 5 mm.

(pers. comm.). However, *Helix seraphinica* we cannot be certain until its anatomy is known, considering the great morphological diversity shown in helicoid shells.

***Eueuhadra* n. gen.**

Type species: ***Eueuhadra gonggashanensis***, n. sp.

Eueuhadra gonggashanensis, n. sp.
(Figs. 7, 28, 34–39; Table 3)

Material

Holotype (IZCAS00067-1), West slope of Gonggashan Mt., Kangding County (30.0°N, 101.9°E), Sichuan Province; coll. De-Niu Chen & Jia-Xiang Gao, 1982-IX-9. Paratypes 14 (IZCAS00067-2–15), the same data as holotype; seven young specimens (IZCAS00067-16–22) were also examined; paratype 1 (IZCAS01061), border of Jiuzhaigou County and Songpan County (33°02'14.4"N, 103°42'32.1"E), Sichuan Province; 3311 m a. s. l.; coll. Min Wu, 2001-X-4.

Etymology

The genus name comes from "eu-" (real) and the bradybaenid genus *Euhadra*. The species is named after the holotype locality: Gonggashan Mountains.

Diagnosis

A simple penis-epiphallus chamber present; dart sac with multiple mucous branches.

Short Description

Shell depressed, dextral, thin but solid. Umbilicus very narrow and more or less covered by columellar margin of the peristome. Protoconch shell granulose.

Penial sheath absent; penis distally with an outstanding tube-shaped penial caecum; epiphallus with a flagellum; a simple penis-epiphallus chamber present; dart sac with a distinct and relatively large accessory sac on the end on which a bundle of mucous glands is inserted per one common duct; accessory sac undivided; in dart apparatus, polylayered structure absent, V1–V4 present.

Range

W China.

Full Description

Shell dextral, depressed, thin but solid. Apex distinct. Whorls convex. Suture impressed.

Umbilicus very narrow and more or less covered by columellar margin of peristome. Columella very oblique. Spiral furrows absent, without ribs, growth lines not accompanied by irregular thickenings, microscopic ripples absent. Protoconch finely granulose, granulation regularly arranged. Teleoconch finely and unevenly granulose on upper spire. Immature shells bluntly angulated. Whorls increasing rapidly; body whorl fairly large, unkeeled,

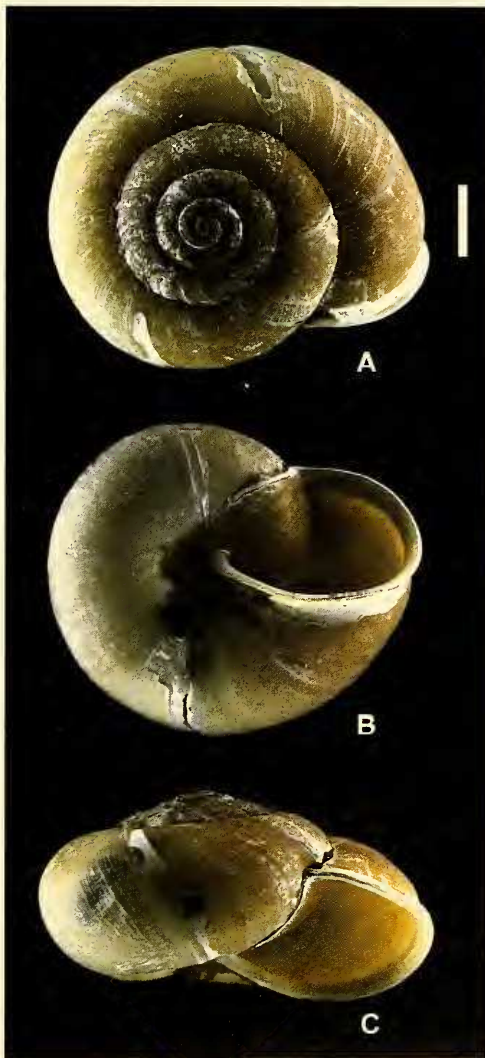


FIG. 34. *Eueuhadra gonggashanensis*, n. gen. & sp., shell, IZCAS00067-1, Holotype, A, apical view; B, basal view; C, apertural view. Bar equals 5 mm.

TABLE 3. Conchological measurements and counts of holotype and paratypes of *Eueuhadra gonggashanensis*, n. gen. & n. sp.

	Shell height	Shell width	No. whorls	No. proto-conch whorls	Apertural length	Apertural width	Umbilicus diameter	Height/width	Umbilicus diameter/shell width
IZCAS00067-1	14.64	24.53	5	1 ³ / ₄	12.46	11.57	1.03	0.60	0.04
	Holotype								
IZCAS00067-2	13.10	23.14	4 ⁷ / ₈	1 ⁷ / ₈	11.67	11.06	0.98	0.57	0.04
IZCAS00067-3	11.91	22.90	4 ³ / ₄	1 ⁷ / ₈	11.69	10.52	1.26	0.52	0.06
IZCAS00067-4	14.08	24.96	4 ⁷ / ₈	1 ⁷ / ₈	13.07	11.01	1.56	0.56	0.06
IZCAS00067-5	12.87	23.28	4 ⁷ / ₈	1 ⁷ / ₈	11.64	10.80	0.72	0.55	0.03
IZCAS00067-6	12.13	22.20	4 ³ / ₄	1 ⁷ / ₈	11.17	9.80	0.94	0.55	0.04
IZCAS00067-7	12.34	23.49	4 ³ / ₄	1 ⁷ / ₈	11.66	10.80	1.20	0.53	0.05
IZCAS00067-8	14.58	26.21	4 ⁷ / ₈	1 ³ / ₄	13.43	11.63	1.29	0.56	0.05
IZCAS00067-9	12.39	22.82	4 ⁷ / ₈	2	11.84	11.27	1.40	0.54	0.06
IZCAS00067-10	12.24	22.65	4 ³ / ₄	1 ⁷ / ₈	11.44	10.67	0.82	0.54	0.04
IZCAS00067-11	11.49	20.48	4 ³ / ₄	2	10.15	9.63	0.93	0.56	0.04
IZCAS00067-12	13.75	23.67	4 ⁷ / ₈	2	12.11	11.10	1.15	0.58	0.05
IZCAS00067-13	12.45	22.78	5	2	11.44	10.18	0.84	0.55	0.04
IZCAS00067-14	11.79	21.96	4 ³ / ₄	1 ⁷ / ₈	10.85	10.10	0.94	0.54	0.04
IZCAS01061	11.05	18.66	3 ⁷ / ₈	1 ¹ / ₄	9.01	9.79	0.59	0.59	0.03
	Paratypes								

slightly descended in front, with convex base. Aperture rather broadly lunate, more or less oblique. Lip toothless, uniformly thickened within, forming a ring-like thickening. Peristome thin, uniformly reflexed. Parietal callus distinct. Periostracum uniformly in greenish brown, bandless. Bottom of body whorl with same or lighter colour (Figs. 34, 35 & 39; Table 3).

Animal with numerous brown spots on the anterior half. Jaw arcuate with 10–12 ribs

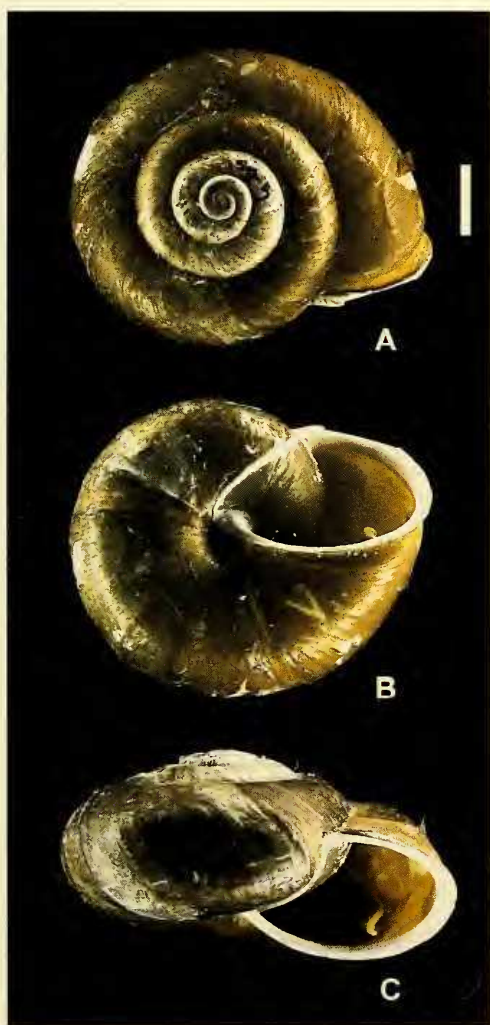


FIG. 35. *Eueuhadra gonggashanensis*, n. gen. & sp., shell, IZCAS00067-5. Paratype, a shell with periostracum on. A, apical view; B, basal view; C, apertural view. Bar equals 5 mm.

dentating the concave margin, ribs wide and almost contiguous. Radula of holotype with 133 rows of teeth, each with one central tooth and 44 lateral teeth on both sides; central tooth with 1 tiny cusp at each side; lateral teeth L_1 – L_{17} , each with an ectocone; L_{18} – L_{31} , each with a tiny endocone and an ectocone; main cones and ectocones of L_{32} – L_{44} bicuspid respectively, two cusps of ectocone roundly blunt (Fig. 36D).

Genitalia: Penial sheath absent (Figs. 7A, 36A, 37A). Penis of moderate length, swollen, with a tube-like penial caecum (PC) near penial retractor. Penial retractor short. Epiphallus thick, short. Epiphallic papilla depressed, symmetrical. Penis internally with three thick penial pilasters and two thinner ones among them (Figs. 36B, 37C). Near to the pore leading to penial caecum, a papilla, built partially by above-mentioned pilasters present (Fig. 7B). Flagellum thick, short, smooth, abruptly tapering and forming a vermiform appendix (Fig. 36A). Penis-epiphallus chamber present, small, simple (Fig. 7E). Vas deferens inserted on flagellum, with inner folds forming a C-shaped open tube towards flagellum (Fig. 7C). Dart sac containing one dart. Dart approximately 2 mm, medially rounded, apically trapezoid in cross section (Fig. 37E, only seen from the spirit material of IZCAS01061; in all dissected specimens of IZCAS00067, the darts are completely eroded, because of having been first fixed in formalin before being preserved in alcohol). Mucous glands longer than dart sac, inserted at the end of accessory sac; with 11–13 (in two specimens of IZCAS00067) mucous lobules radially arranged, stalk of lobule indistinct; each lobule simply branched and consisting of slightly expanded vesicles, not expanded distally (Fig. 36A). Accessory sac developed, innerly simple except for some narrow pilasters; a bundle of mucous glands inserting on the end of AS, from a common entering tube, its inner entrance without papilla (Fig. 7D); ADC share the same entrance with DtC; V1–V4 present; V1, V2 and V4 forming DtC; C23 present and tiny, with entrance leading to ADC (Figure 7D). DVM absent. Poly-layered structure (PLs) absent. Bursa copulatrix ovate, not well differentiated from bursa copulatrix duct (Fig. 36A). Bursa copulatrix duct of moderate length, wide, inserting high on vagina (Figs. 36A, 37A). Ovotestis palm-shaped, distinctly branched and two stalks closely arranged and having a common duct; in holotype, ovotestis embed-

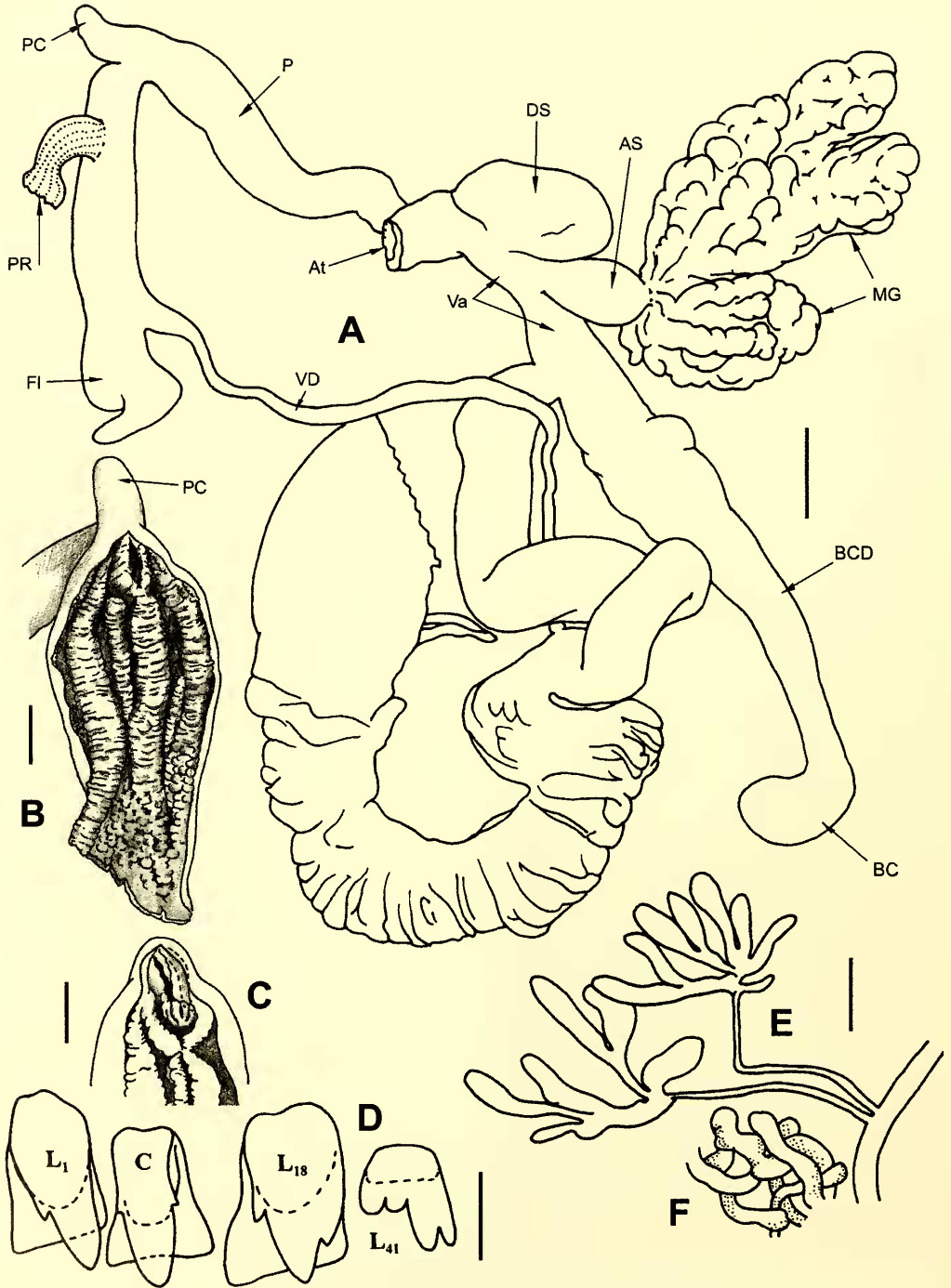


FIG. 36. *Eueuhadra gonggashanensis*, n. gen. & sp., IZCAS00067-1, Holotype, A, general view of genitalia, bar equals 2 mm; B, penis, opened; C, penial caecum, opened; D, teeth of radula, bar equals 25 μ m; E, a leaf of ovotestis, bar equals 0.5 mm; F, ovotestis matrix, magnified. B, C, bars equal 1 mm.

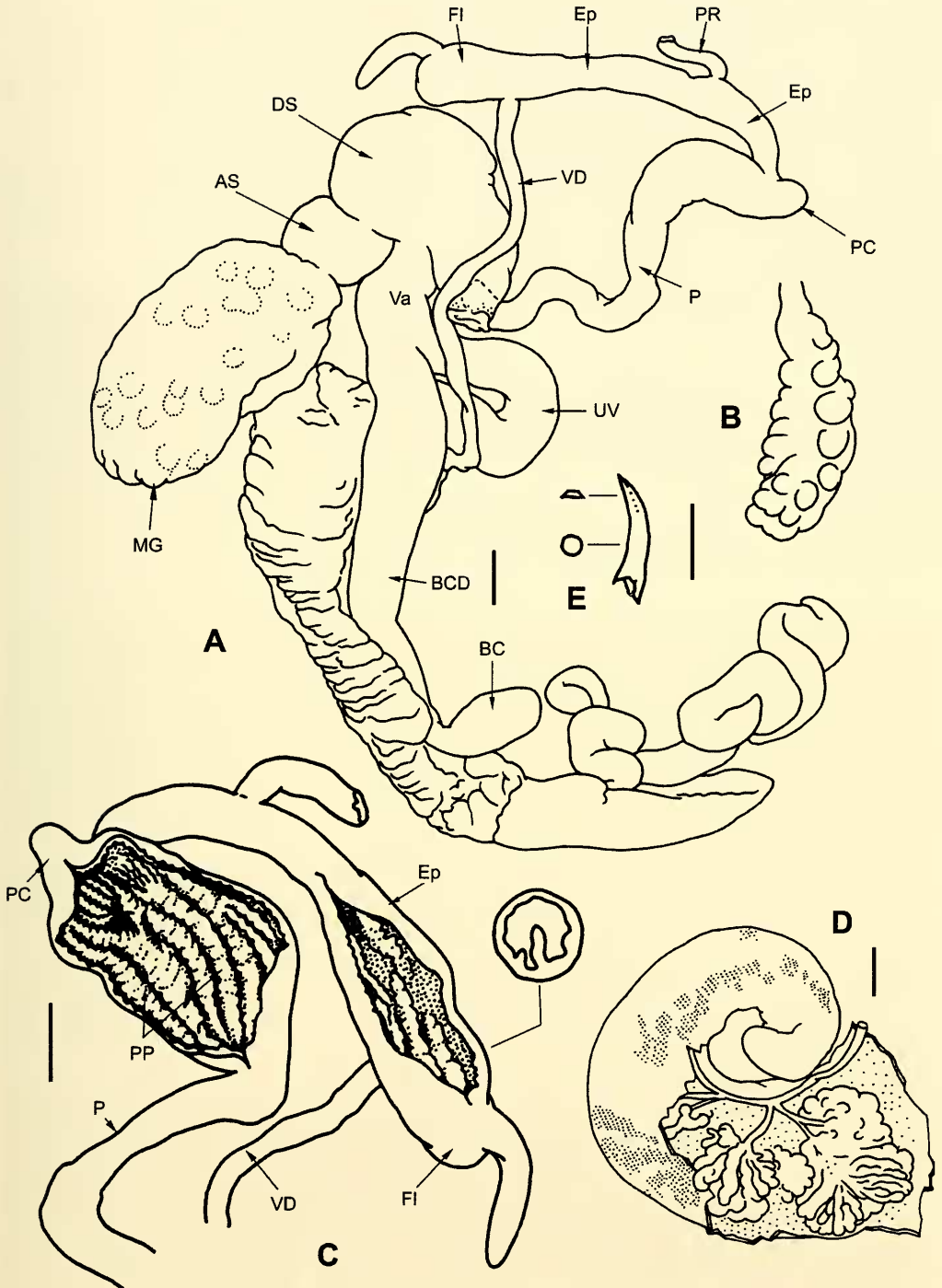


FIG. 37. *Eueuhadra gonggashanensis*, n. gen. & sp., genitalia, IZCAS01061, paratype, A, general view of genitalia; B, a branch of mucous glands; C, penis, penial caecum (PC), and flagellum, opened; D, ovotestis; E, dart with cross sections. Bars equal 1 mm.

ded in matrix composed of disordered fibers (Fig. 36F; in the other examined specimens the matrix normal); stalks fairly long (Figs. 36E, 37D). Holotype: dart sac 3.3 mm in length, 1.8 mm in width, ratio of width to length 0.5; mucous duct length 7.3 mm; vagina length 4.6 mm; free oviduct 12.2 mm; bursa copulatrix duct length 10.3 mm, bursa copulatrix duct basal width 1.5 mm; transverse diameter (maj.) of bursa copulatrix 1.5 mm, sagittal diameter (maj.) 2.2 mm; vas deferens length 13.7 mm; penis length 7.0 mm; epiphallus 6.4 mm; flagellum length 3.0 mm; PR length 2.2 mm.

Range

Western Sichuan, the species was known only from two localities where type and holotype material were collected (Fig. 28).

Remarks

This species differs from all known bradybaenids by having a simple penis-

epiphallus chamber. The sisterhood of this species and *Aegistohadra delavayana* (Heude, 1885), n. gen. & comb., is suggested by their common derived character the penial caecum.

Ecology

This species (IZCAS01061) inhabits high mountains (Fig. 38B), in very low density. The environment is extremely wet, inside a dark fir forest, where the stones and fallen trunks are covered by a thick layer of lichen and moss which sometimes reaches the thickness of approximately 50 cm (Fig. 38C, D). The specimen (IZCAS01061), the only collection after careful search of about 500 m² in the forest was found inactive under moss. The population in Jiuzhaigou seems to be isolated from another known population in the Gonggashan Mountains. Based on 30-days field work covering the area from Dujiangyan to Jiuzhaigou along Minjiang River, it has been confirmed that these two populations are fairly sepa-

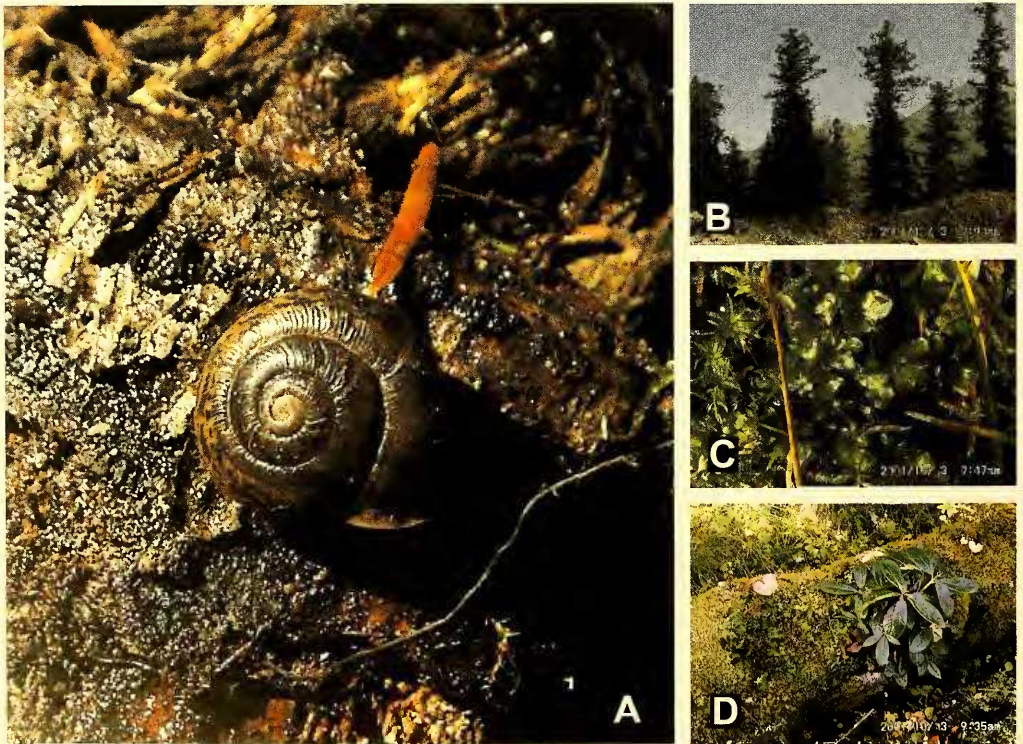


FIG. 38. Habitat of *Eueuhadra gonggashanensis*, n. gen. & sp. A, Paratype, IZCAS01061, in its habitat; B–D, natural environment conditions of locality for Paratype IZCAS01061.

rated. In the same area, no helicoid snails were found and only the non-helicoid snail *Deroceras (Deroceras) altaicum* (Simroth, 1886) (Wiktor et al., 2000), which is widely distributed in the whole vally of Minjiang River and its neighboring mountains. It is also interesting that no conchologically similar species was recorded in this region before (e.g., Pilsbry, 1934).

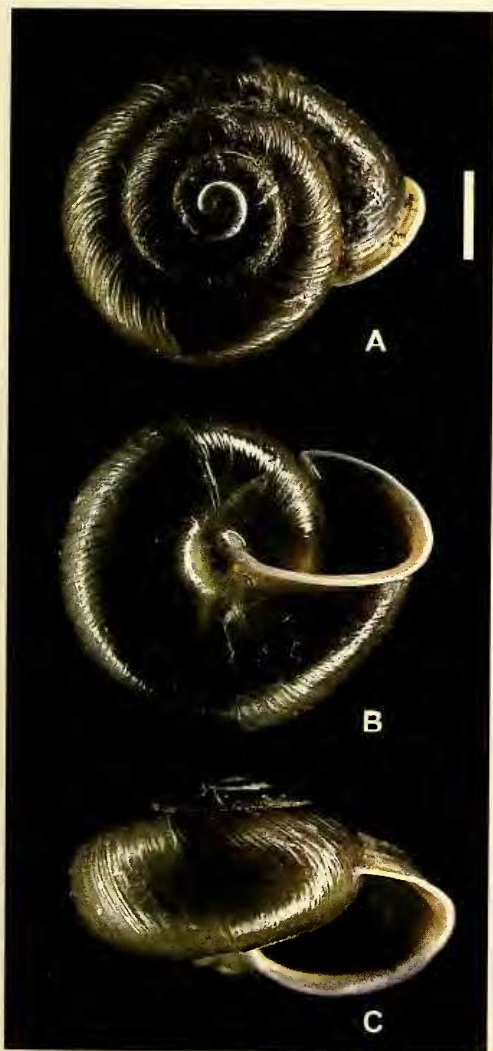


FIG. 39. *Eueuhadra gonggashanensis*, n. gen. & sp., shell, IZCAS01061, paratype, A, apical view; B, basal view; C, apertural view. Bar equals 5 mm.